University of Alberta

Effects of Soil Temperature and Water Table Level on *Picea glauca*, *Betula papyrifera*, *Populus tremuloides* and *Populus balsamifera* seedlings

by

Gwen Bridge

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Effects of Soil Temperature and Water Table Level of *Picea glauca*, *Betula papyrifera*, *Populus tremuloides* and *Populus balsamifera* seedlings, submitted by Gwen Bridge in partial fulfillment of the requirements for the degree of Master of Science in Forest Biology and Management.

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Abstract

I studied the effect of various water tables and soil temperatures on growth and transpiration of *Populus tremuloides* Michx., *Populus balsamifera* L., *Betula papyrifera* Marsh. and *Picea glauca* (Moench) Voss to evaluate the potential of using deciduous species for control of high post-harvesting water table levels on boreal sites. A growth chamber experiment indicated that *Betula papyrifera* was able to maintain higher rates of transpiration than the other species at high water tables, especially at cold to moderate soil temperatures. In a field experiment conducted near Slave Lake, Alberta, *Populus balsamifera* utilized more water and maintained a high leaf area compared to the other species during a very wet year. The comparative responses of *Populus balsamifera* and *Betula papyrifera* to high water tables indicate that they are the most suitable species to plant where water table rise may occur on boreal mixedwood sites after harvesting.

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Chapter 1. Introduction

Regeneration after disturbance in the boreal forest is a complex process involving establishment and growth of various trees, herbs, and grasses. Different establishment and growth strategies along with the effects of environmental variables on that growth ultimately determine both survival of individual plants and different species groups. Of the key environmental variables, which include soil and air temperature, water, nutrients, and light, water plays a critical role in the growth of various species and thus on the composition of boreal vegetation communities. Understanding the comparative ability of early successional species to persist in the presence of excess water is essential when attempting to reestablish, based on a natural disturbance regime, a commercially viable forest where a rise in water table follows a canopy-reducing disturbance.

Silvicultural management strategies

Forest management dramatically impacts boreal forest ecology. Clearcut harvesting is often the preferred method for harvesting productive mixedwood forest dominated by *Populus tremuloides* Michx. and *Picea glauca* (Moench) Voss with more minor components of *Populus balsamifera* L. and *Betula papyrifera* Marsh. Clearcut harvesting often results in a rise in water table in boreal forest sites (Heikurainen 1967, Holstener-Jorgensen 1967, Dubé and Plamondon 1995). After harvesting, prevailing silvicultural methods involve an attempt to regenerate *P. glauca* trees as quickly as possible. This strategy often requires expensive intervention, such as mechanical or chemical site preparation, and manual brushing or herbicide treatments to aid *P. glauca* regeneration through control of vegetative competition. However, pursuit of this strategy does not usually address the issue of high water tables. *Picea glauca* is not well adapted to high water table environments (Levan and Riha 1986) and open canopy conditions (Man and Lieffers 1997) and therefore does not survive well in wet open sites (Eis 1967).

Natural successional patterns in the boreal forest

Natural succession on disturbed boreal sites begins with establishment of pioneer species that include herbs, shrubs, and trees. Early successional species that occur on disturbed boreal sites with high water tables often include *P. balsamifera*, *P. tremuloides* and *B. papyrifera* (Mallick et al. 1997). Because of their rapid growth and leaf area development these hardwoods may prepare sites for subsequent succession of other species by reducing the water table level. Ackzell (1994) found that deciduous pioneer species often occur on wet sites after a disturbance such as scarification has occurred. Similarly, Roy et al. (2001) and Mallick et al. (1997) found that after clearcutting and a rise in water table, pioneer deciduous species (*P. tremuloides,* and *B. papyrifera*) invade the sites, but these trees can hinder conifer regeneration through competitive effects. The fact that these early successional species are persistent in their ability to establish and grow on these sites suggests that they are suitable for re-establishing a natural successional pattern on disturbed sites. Such trees could begin to reduce the water table through biological means, blunting the need for artificial drainage to reduce water table elevations as was proposed by Roy et al. (2001). Furthermore, *P. glauca* has good survival and early growth on prepared planting mounds under an aspen overstory (DeLong et al. 1997).

An additional factor on these wet sites can be the presence of *Calamagrostis canadensis*, which is a pioneer grass species. Once *C. canadensis* becomes established, it is an effective agent inhibiting regeneration and growth of conifers (Lieffers et al. 1993) and reducing growth of deciduous trees such as *P. tremuloides* (Landhäusser and Lieffers 1998). However, growth of *Calamagrostis canadensis* can be reduced by shade under a partial *P. tremuloides* canopy (Lieffers et al. 1993). Thus the early regeneration of a vigorous canopy of deciduous species could also aid in preventing site dominance by *Calamagrostis canadensis*, in addition to reducing the water table level through increased interception, evaporation and transpiration of water. Reduced grass competition and increased shade would also be conducive to *P. glauca* regeneration as it is a shade adapted species able to grow under a deciduous canopy (Fries et al. 1997).

The effect of woody vegetation (trees and shrubs) on reducing groundwater table levels has been previously established by several researchers (LeMaitre et al. 1999, Holstener-Jorgensen 1967). Leaf area can be quickly re-established by early successional species. In as little as ten years after disturbance, Kochenderfer and Wendel (1983) observed that the evapotranspiration losses from a ten year-old stand of regenerating vegetation reached the same level as that of a 60 – 100 year old stand of hardwood vegetation. This suggests that *P. glauca* regeneration does not need to be delayed as a result of a high water table until a deciduous canopy nears maturity. Regeneration after fire disturbance on *P. glauca* sites involves *P. glauca* co-regenerating with hardwoods (Zasada 1994). In fact, *P. glauca* shares some attributes with pioneer species such as the ability to establish quickly under some conditions. Unlike most pioneer species however, *P. glauca* is able to establish under a canopy (Dix and Swan 1971) and continues to grow for decades (Lieffers et al. 1996). If the overstory of aspen is harvested between 26-45 years, the growth rate of *P. glauca* is increased considerably (Yang 1991). Dix and Swan (1971) observed natural release of *P. glauca* from competition with aspen. They reported no *P. balsamifera, P. tremuloides* and *B. papyrifera* trees older than 60 years in their study of boreal forest disturbance succession and showed that *P. glauca* establishes early after a disturbance and remains living after the early successional species have died. However, Zasada (1994) found that *P. glauca* can occur in mixed stand with hardwoods for up to 100 years. A complementary observation supporting the theory that conifer regeneration is aided by early successional species comes from Huikari (1959) who showed that *P. abies* and *Pinus sylvestris L.* had higher survival when grown with *Betula verrucosa* (Ehrh.) and *Betula pubescens* (Ehrh.).

If management strategies were modified to include both deciduous and spruce trees on one site, the potential for two crops in a single mixedwood stand exists. Under-planting the deciduous canopy with *P. glauca* may be necessary to ensure successful softwood establishment. The reduced need for herbicide and brush control treatments could lower silvicultural costs, and an additional monetary benefit could be gained from two crops in a single, though lengthened, rotation. The inclusion of deciduous pioneer species to the silvicultural prescription for *P. glauca* mixedwood site regeneration is consistent with

natural ecology and disturbance succession patterns thought to be present on these sites. In fact, hardwood inclusion has been part of Swedish forest policy since 1993 for management of Norway spruce forests that are characterized by initial deciduous pioneer regeneration, along with the recognition that rotation periods need to be extended from 80-120 years to 100-200 years (Fries et al. 1997). Preventing the regeneration of deciduous species also results in the loss of the deciduous component that offers specialized habitats for some insects and nonvascular plants species (Fries et al. 1997, Crites and Dale 1998, Hazell et al. 1998). In the discussion of the importance of mixedwood management in the boreal forest, MacIsaac et al. (1999) predicted that in the next 30-50 years, *P. glauca* trees that developed in natural succession under hardwood overstory will be an important component of the overall commercial harvest of *P. glauca*.

Flooding tolerances of boreal tree species

Various physiological and morphological changes occur in plants when they are exposed to flooding including severe reduction in photosynthesis, growth, and death of roots (Kozlowski 1984). Photosynthetic rate of trees is reduced by saturated soils (Peterson and Bazazz 1984). During flooding, root respiration becomes anaerobic and the result is a build up of toxic constituents such as ethylene, ethanol, hydrogen sulfide and other chemicals (Kozlowski 1979). This results in negative effects on the physiology and growth of plants. For example, ethylene can produce leaf epinasty, leaf senescence and abscission (Pereira and Kozlowski 1977). Additionally, in an anaerobic environment, mineral uptake is reduced due to lack of energy for such processes, thus the plant also suffers from a lack of mineral nutrition.

Picea glauca is a boreal species that is known for it's general lack of flooding tolerance. Mueller-Dombois (1964), Grossnickle (1986), and Reece and Riha (1991) all observed a reduction in stomatal conductance and height and root growth in flooded soils. Extended periods of flooding (>29 days) resulting in death of white spruce trees in Minnesota was observed by Ahlgren and Hansen (1957). Variable tolerance to flooding has been reported for other boreal trees. For instance, Tang and Kozlowski (1983) reported

strongly reduced growth of flooded *B. papyrifera* compared to non-flooded seedlings and Ahlgren and Hansen (1957) reported that *B. papyrifera* was the least flooding tolerant of the hardwood species that occur in the boreal forest, including *P. tremuloides* and *P. balsamifera.* In contrast, in a study of wetland tree species, Dang (1992) found that *Betula pumila* was better adapted to flooded soil conditions than both *Larix laricina* and *Picea mariana*. Similarly, Amlin and Rood (2001) reported that inundation reduced growth and transpiration of *P. balsamifera* and similar findings (including reduction of photosynthesis) were reported for *Populus deltoides* by Regehr et al. (1975). Kranjcec et al. (1998) compared growth of *P. balsamifera* to other *Populus spp.* and found that its growth was much more vigorous than that of the other species across a range of water table levels, including flooded conditions (5cm below the surface). Less is known about the relative flooding tolerance of *P. tremuloides,* although it is commonly observed to colonize wet harvested sites (Roy et al. 1995).

Responses of boreal tree species to cold soil temperatures

It is generally accepted that cold soil temperatures reduce tree water uptake and gas exchange, and thus reduce growth (Kramer 1969, Lopushinsky and Kaufmann 1984, Lopushinsky and Max 1990, Iivonen 1999, Vapaavouri et al. 1992, Wan et al. 1999). If cold soils occur during plant growth, desiccation can result from the transpiration demand exceeding the capacity of roots to take up water (Kramer 1969). Temperatures remain cold longer in soils that are heavy textured and poorly drained, which is the case in many boreal sites. Water absorption at low temperatures is thought to be reduced due to the higher viscosity and therefore decreased permeability of the root cells to water (Kramer 1969).

In cold soils, coniferous trees generally have greater root growth and survival than deciduous trees (Tyron and Chapin, 1983, Landhäusser et al. 2001, Heninger and White 1974). Heninger and White (1974) found the optimal soil temperature for white spruce was 19 °C compared with an optimum soil temperature for birch of 23-31 °C with growth and survival becoming limited at 15°C. These temperatures are high compared to soil

temperatures characteristic of boreal sites. Furthermore, temperature and flooding often have strong interaction effects on growth that ultimately govern how well trees might perform under variable field conditions. For example, Lieffers and Rothwell (1989) observed positive growth responses in *Picea mariana* and *Larix laricina* under high water table conditions, but negative responses under lower water table conditions. Lieffers and Rothwell (1986) explained this interesting result as a likely effect of slowed down bacterial activity and thus improved soil aeration in the flooded soil at cold soil temperature. Though the relative tolerances to the individual effects of flooding and cold soils are understood for many tree species (including many boreal species), the combined effects of these two variables on physiology and growth of tree species commonly found on boreal sites is generally less well understood. This understanding is needed in order to design silvicultural strategies that more closely interpret natural successional patterns for boreal forest stand establishment and growth.

Research objectives

Since water table level reduction after disturbance is an important component of forest regeneration, a basic question in my research was to determine which of the common boreal species has the greatest initial potential to use the most water. I considered four boreal tree species for this research: *P. tremuloides*, *P. balsamifera*, *B. papyrifera* and *P. glauca*. If early successional species are to be planted, knowing which species has the greatest potential to control water table elevation would be valuable in planning silvicultural strategies for *P. glauca* regeneration. Success of silvicultural prescriptions based on a natural regeneration model will be greatly enhanced by this type of species specific information. This type of information has been lacking in the literature and is currently a barrier to the successful implementation of such strategies (Bergeron et al. 1999).

The overall objectives of my research were to determine the comparative water use of four boreal tree species in wet and potentially cold site conditions by measuring growth, and transpiration and total sapflow of seedlings in both a growth chamber environment

and in the field. In chapter 2, I report on a growth chamber study investigating the comparative effect of two water table levels and three soil temperatures on the growth, transpiration and net assimilation of young seedlings of these four boreal species. In chapter 3, I report on a field study in which I planted seedlings of these four boreal species in a mesic to wet clearcut where an increase in water table had occurred following harvesting. Daily sapflow (transpiration) and tree growth in two micro-site conditions over two growing seasons were used to evaluate the comparative water use of these species. In Chapter 4, I compare results from the two studies and outline some possible silvicultural applications of the research results.

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Chapter 2. Growth, transpiration, and net assimilation of *Picea glauca* (White spruce), *Populus tremuloides* (Aspen), *P. balsamifera* (Balsam poplar) and *Betula papyrifera* (White birch) at various water tables and soil temperatures

Introduction

Cold, wet site conditions are common after harvesting of poorly drained *Picea glauca* (Moench) Voss (white spruce) from mixedwood stands in boreal regions (Dubé et al. 1995). A high post-harvest water table results from removal of the transpiring overstory trees and loss of intercepting canopy. Post-harvesting water table rise or "watering up" creates problems for regenerating *P. glauca* (Eis 1967, Leven and Riha 1985). In addition, *Calamagrostis canadensis* (Michx.) Beauv. begins to dominate many of these sites; out-competing both naturally regenerated and planted coniferous tree seedlings (Lieffers et al. 1993). A possible silvicultural solution to poor *P. glauca* seedling survival on wet sites may be to allow planted or naturally regenerated deciduous species to control the high post-harvest water tables and grass establishment. If deciduous pioneer tree species can quickly produce sufficient leaf area and re-establish transpiration losses under cold-flooded conditions, they may be able to lower the water table to restore favorable rooting conditions for *P. glauca* regeneration. I conducted a growth chamber study to determine which of several boreal species has the greatest potential for reducing water table through production of a large leaf area and maintenance of a high transpiration rate.

Many growth chamber/greenhouse studies have compared the effects of flooding on various conifers (Levan and Riha 1985, Reece and Riha 1991) and deciduous trees (Harrington 1987, Amlin and Rood 2001, Ranney and Bir 1994, Tang and Kozlowski 1983, Tang and Kozlowski 1982). Controlled temperature experiments have also been conducted on both coniferous and deciduous tree species (Ryyppö et al. 1998, Vapaavuori et al. 1992, Landhäusser et al. 2001, Tyron and Chapin 1983, Heninger and White 1974). However, the combined effects of both temperature and flooding on tree

physiology and growth have been less well studied in controlled environments. Examples of the latter include Lieffers and Rothwell (1986) who studied *Picea mariana* (Mill) B.*S.P.* and *Larix laricina* (Du Roi) K. Koch. and Tsukahara and Kozlowski (1986) who studied *Betula platyphylla* var. *japonica* Hara..

Flooding alone has negative effects on growth of many tree species (Kozlowski, 1997). Flooding affects trees by reducing the available oxygen in the soil, which results in stomatal closure and associated decreases in root water uptake (Kozlowski, 1985). The process of stomatal closure in a flooded plant is to a large extent controlled by ethylene. Ethylene stimulates both leaf abscission and stomatal closure. Ethylene is particularly implicated in the response to flooding by the part of the tree above ground. Ethylene is produced in the roots of flooded trees and transported to leaves and is thought to trigger stomatal closure in flood intolerant species (Kozlowski 1997, Kozlowski and Pallardy 1997). Though considerable variation in flooding tolerance exists among species, angiosperms are generally considered more flooding tolerant than gymnosperms (Kozlowski 1997).

In addition to the physiological effects of flooding, cold soil temperatures (i.e. $\leq$10°C) commonly found in the boreal forest may have either a beneficial or negative effect on tree growth. Lieffers and Rothwell (1986) suggest that cold soil temperatures may be beneficial to *P. mariana* and *L. laricina* in flooded conditions because cold temperatures may slow the activity of anaerobic microbes responsible for decomposition of organic matter. On the other hand, cold soil temperatures can also inhibit tree growth and transpiration (Nambiar et al. 1979, Wan et al. 1999, Vapaavuori et al. 1992, Lopushinsky and Max 1990). Cold soils decrease the permeability of roots to water and also increase water viscosity, thereby increasing hydraulic resistance through the soil and roots (Kozlowski and Pallardy, 1997). Although research has been conducted on the effects of either flooding or temperature on growth of boreal tree species (Tang and Kozlowski 1982, Tang and Kozlowski 1983, Iremonger and Kelly 1988, Tripepi and Mitchell 1984, Zaerr 1983, Heninger and White 1974, Landhäusser et al. 2001), and on the effects of both soil temperature and water table level (Lieffers and Rothwell 1986, Tsukahara and

Kozlowski 1986), to my knowledge comparative information on the effects of flooding and soil temperature among common upland boreal trees has not been well studied.

The objective of this study was to assess the responses of four boreal tree species to variation in water table level and soil temperatures to determine their suitability for managing water table level in harvested wet mixedwood sites. The hardwoods, *Populus tremuloides* Michx., *P. balsamifera* L. and *Betula papyrifera* Marsh. pioneer disturbed sites in northern Alberta, and *P. glauca* exploits a later successional stage (Dix and Swan 1971). I hypothesized that *P. tremuloides*, *P. balsamifera* and *B. papyrifera* would transpire more water under flooded conditions than *P. glauca* due to their larger leaf areas and relatively rapid growth rates. *P. balsamifera* and *B. papyrifera* are often found in poorly drained soils or riparian areas and this suggests their tolerance to high soil moisture conditions. All three deciduous species are also found rapidly colonizing disturbed boreal forest areas that have high water table levels. This further supports the hypothesis that the deciduous species may be more flooding tolerant than the later successional *P. glauca*. *Picea glauca* is not considered to be tolerant to flooding (Mueller-Dombois 1964). My second hypothesis is that these deciduous trees transpire more water per unit leaf area under cold temperature conditions. Of the three deciduous species, *B. papyrifera* has the widest distribution in Canada and northern United States, followed by *P. balsamifera* and then *P. tremuloides* (Farrar 1995). Their wide northerly distribution indicates that these three species are tolerant to cold soils. Also, Tyron and Chapin (1983) have shown that deciduous boreal species achieve better growth rates in cold soils than coniferous species when tested in a laboratory.

Materials and Methods

Plant material and growing conditions

Seedlings of *B. papyrifera*, *P. tremuloides*, *P. balsamifera* were grown from seed collected locally in Edmonton, Alberta, 53° 33' 00" N - 113° 28' 00" W, in March 1999. Dormant *P. glauca* seedlings (one year old) were obtained from a local commercial grower. Seedlings were grown in 6-15 styroblocks (Beaver plastics, Edmonton, AB).

Growth chamber conditions were 20°C/18°C, with 18h/6h light/dark cycles with a relative humidity of 60%. Plants were watered when required and fertilized every two weeks with commercial fertilizer (2 g l^{-1} of 20-20-20 N-P-K with chelated micronutrients). After four months of growing in styroblocks, seedlings were transplanted into pots constructed of ABS plastic pipe sections 30 cm long and 10 cm in diameter. Landscape cloth secured over the pipe bottoms with elastic bands allowed for water drainage after watering. Soil in both the styroblocks and pipes was a sand/peat mix (2:1 v/v). After about 4 months of growing in the ABS pipe pots, the seedlings were moved outside (Oct. 1999) for six weeks to harden them off. After hardening, the seedlings were brought back inside and stored under dark and cool conditions for four weeks. During this period, the stems of the deciduous species were pruned to approximately 30 cm in height.

In December 1999, the ABS pipe sections were fitted with a watertight end-cap, and a 4 cm diameter by 30 cm long ABS plastic pipe was taped to the side of the larger 10 cm diameter pipe containing the plant. A flexible plastic tube connected the large pipe to the small pipe at the base of the pipe sections. The flexible tube allowed water to pass freely between the two pipes (Figure 2-1). The smaller diameter pipe functioned as a water reservoir. The water table was maintained at either a high level, 9.8 cm from the soil surface, or a low level, 23 cm from the soil surface by filling the smaller pipe with water to the desired level. Half of the seedlings of each species received the high water treatment and half received the low water treatment.

Within each water level treatment, six to eight seedlings per species were assigned to each of three soil temperature treatments (7.5, 12, and 22°C). To control soil temperature, the pots were submerged in water baths consisting of watertight plywood boxes (90x90x46 cm). For the two low soil temperature treatments (7.5 and 12°C), water was chilled with two circulating coolers (one for each temperature) stored in insulated reservoirs and then pumped to the water baths (Figure 2-1). An overflow pipe returned the warmer surface water back to the cooling unit. For the 22°C soil temperature, an electrical heating element was used to maintain the water temperature. Soil temperature

was regulated with thermostats throughout the experiment and monitored regularly with thermometers. The plants were fertilised every two weeks with a commercial fertilizer ($2g \cdot l^{-1}$ of 20-20-20 N-P-K with chelated micronutrients). The growth chamber conditions were maintained at 20°C/18°C, with 18h/6h light/dark cycles and a relative humidity of 60%. During the growing period the pots were randomly relocated within soil temperature treatment boxes to compensate for possible spatial differences in growth chamber conditions.

After 6 weeks, physiological and growth variables were measured on the seedlings. Mortality during this period (presumably due to treatment effects) reduced the number of seedlings in some species x treatment combinations. Another factor in *P. balsamifera* seedling mortality may be that several of the seedlings did not flush and a black stem fungus was evident on several others. This reduced sample size for *P. balsamifera* in some treatment combinations (Table 2-1). *Populus tremuloides* seedlings also had limited survival in the cold soil treatment (3-4 seedlings). All other treatment combinations had 5-8 seedlings per treatment combination (Table 2-1), except *P. tremuloides* in the 22°C and high water table treatment and *P. balsamifera* in the 22°C and low water table treatment which both had five seedlings.

Measurements

Growth variables (total leaf area, leader growth, root dry weight/shoot dry weight ratio, live root dry weight), were measured on all seedlings.

For the deciduous species, projected leaf area was determined using a leaf area meter (LI-3100, Li-Cor Ltd. Lincoln, NE, USA). Projected *P. glauca* leaf area was estimated using a relationship between needle dry mass and projected needle area of sub-samples measured using a computer scanner and imaging software (Sigma Scan 3.0, Jandel Scientific, San Rafael, CA, USA). For *P. glauca*, leaf area was calculated using only the needles on new shoots (i.e. produced under the treatment conditions). Roots were then carefully washed over a sieve to remove the soil from the roots and dead roots were

separated from the live roots. All biomass samples were dried at 68°C for 48 hours and then their dry weight was determined. Leader length was measured with a ruler from the origin of the leader to the tip of the shoot.

Transpiration and net assimilation rates were measured on the actively growing seedlings (mature leaves) with an open-system infrared gas analyser (IRGA, CIRAS I, PP Systems, Haverhill, Mass.) with a broadleaf cuvette (Auto cuvette, PP systems, Haverhill, Mass., USA) for *P. tremuloides*, *P. balsamifera* and *B. papyrifera*, and for *P. glauca*, on the terminal leader (new growth) with a conifer cuvette (Auto cuvette PP systems, Haverhill, Mass., USA). Light, leaf temperature, and relative humidity were maintained at 1000 $\mu mol\ m^{-2}\ s^{-1}$ (PAR), 20° C, and 35%, respectively.

Statistical analysis

Analysis of variance (ANOVA) was performed on the growth and gas exchange data to determine treatment effects on each species individually. The data was analyzed as a randomized 3 × 2 factorial design (treatments were fixed effects) with 3 soil temperatures (7.5, 12, and 22°C) and 2 water levels (9.8 and 23 cm depth from surface). Differences between species (relative response of species to water table and soil temperature treatments) were explored qualitatively by comparing the relative strength of treatment effects among species. Variables were tested using Levene's test (ANOVA on absolute deviation) to confirm the assumptions of normality and homogeneity of variance. Data not meeting the homogeneity of variance assumptions were log transformed (transpiration and net assimilation for *B. papyrifera* and *P. balsamifera*, leaf area and live root weight for *P. tremuloides*, live root weight for *P. balsamifera*, and root:shoot ratio for *P. balsamifera* and *B. papyrifera*). Log transformation was used for significance determinations but actual values were used for illustrative purposes. Differences among temperature treatment levels were compared using multiple range tests if a significant F-test was observed. Significance levels for multiple range tests were set at $\alpha=0.05$. Temperature levels were compared using Tukeys HSD test (in the case of equal n among levels), and the Spjotoll/Stoline test was used in the case of unequal n among temperature

levels. All statistical analyses were performed using the STATISTICA software program (StatSoft 2300 E. 14th Street, Tulsa, OK).

Results

Seedling growth variables

Leaf area of all species was greatest in the low water table level treatment (Figure 2-2a). Within species, differences in leaf area between water table treatments were greatest for *P. glauca* ($p=0.008$) and *P. balsamifera* ($p=0.024$). Though not statistically significant, moderate effects of water table level on leaf area of *B. papyrifera* ($p= 0.108$) and *P. tremuloides* ($p= 0.085$) were observed. Leaf area of *P. tremuloides*, *B. papyrifera* and *P. balsamifera* was significantly reduced by the cold soil temperature treatment (Figure 2-2b). Leaf areas were larger for *P. tremuloides*, *B. papyrifera* and *P. balsamifera* in the high temperature treatment than in the cold temperature treatment ($p=0.025$, $p<0.001$, and $p=0.005$, respectively). In contrast, the leaf area of *P. glauca* was unaffected by soil temperature ($p=0.64$). No interaction effects between water table and soil temperature treatments on total leaf area growth for deciduous trees and new leaf area for coniferous trees were observed for *P. tremuloides*, *B. papyrifera* and *P. glauca*. However, the very large leaf area of *P. balsamifera* in the 22 °C and low water table level treatment combination resulted in an interaction effect ($p=0.015$).

Live root dry mass of *P. balsamifera* and *P. glauca* were greater in the low water table treatment ($p=0.028$ and $p<0.001$, respectively) (Figure 2-3), while live root masses of *B. papyrifera* and *P. tremuloides* were not affected by water table level (Table 2-2). No effect of soil temperature was observed on the live root mass of any of the deciduous seedlings (data not shown). *Picea glauca* live root mass was increased only at the low water table treatment x 22 °C soil temperature, which resulted in a significant interaction effect between water table level and soil temperature ($p<0.001$) (Figure 2-4).

Root:shoot ratios were not affected by temperature or water table level treatments in any of the deciduous seedlings (Table 2-2). However, significant ($p<0.001$) effects of both water table level and soil temperature on root:shoot ratio were observed in *P. glauca*. The strength of these main effects was largely produced by the 22°C soil temperature x low water table level treatment combination in which the root:shoot ratio of 0.55 was nearly double that of the other treatment combinations (0.17 to 0.28) resulting in a strong interaction effect ($p<0.001$, Table 2-2). Below ground growth of *P. glauca* responded positively and strongly to the higher temperature and the lower water table level treatments.

Higher soil temperatures resulted in greater leader length in deciduous species. Leader growth of *P. tremuloides* was greater in the 22°C than in the 7.5°C soil treatment ($p=0.008$) and *B. papyrifera* leader growth was greater in both the 22°C and the 12°C than the 7.5°C, ($p=0.004$). *Populus balsamifera* leader growth increased as soil temperature increased ($p=0.005$); *P. balsamifera* leader growth was least in the 7.5°C treatment, and less in the 12°C, than in the 22°C treatment. Water table had a significant effect on leader growth of *B. papyrifera* and *P. glauca*, which increased in response to a low water table ($p=0.043$ and $p=0.014$, respectively; Table 2-2). No interaction effects were observed for any of the species.

Gas exchange

Net assimilation rates (NA) of all species except *B. papyrifera* were affected by water table treatments (Figure 2-5a). Photosynthesis was approximately 3 times higher in the low water treatment compared to the high water table treatment in *P. glauca*, *P. tremuloides* and *P. balsamifera* ($p<0.001$), while a weaker, but statistically non-significant difference (2 fold) was observed in *B. papyrifera* ($p=0.107$). Net assimilation was greater at higher soil temperatures in all species. *Betula papyrifera* NA rate was lower in the 7.5°C soil treatment than at 12 and 22°C ($p=0.016$). *Picea glauca* and *P. tremuloides* also responded to soil temperature with higher NA in the 22°C soil temperature than in the 7.5°C treatment ($p=0.039$, $p=0.011$ respectively; Figure 2-5b). An interaction effect between the soil temperature and water table level on NA was

observed for *P. glauca* ($p<0.001$) and *B. papyrifera* ($p=0.002$). Net assimilation rates of *P. glauca* seedlings in the low water table condition were generally higher than those in the high water table treatment. However, *P. glauca* seedlings in the high water table treatment and 12°C soil temperature had NA rates 1.5 times higher than seedling in the high water table and 7.5°C treatment and 2 times higher than seedlings in the high water table and 22°C treatment. But in the low water table, *P. glauca* NA was almost double in the 22°C treatment, 6.91 μmol m^{-2} s^{-1}, when compared to NA in the 12 and 7.5°C treatments, 3.90 and 3.97 μmol m^{-2} s^{-1}, respectively ($p<0.001$ interaction effect). *Betula papyrifera* generally performed better at the lower soil temperatures (7.5 and 12°C) when water table was high ($p=0.002$ interaction effect). Indeed, the lowest *B. papyrifera* NA (1.3 μmol m^{-2} s^{-1}) was measured at a high water table treatment and a soil temperature of 22°C. No significant interaction effects between water table level and temperature on NA were observed for *P. balsamifera* or *P. tremuloides* (Table 2-3)

Transpiration rates of *P. glauca*, *P. tremuloides*, and *P. balsamifera* were greater in the low water table compared to the high water table treatment ($p<0.001$ for *P. glauca*/*P. tremuloides*, and $p=0.015$ for *P. balsamifera*; Figure 2-6a). However, no effect of water table level on transpiration was observed for *B. papyrifera* ($p=0.89$). Increases in soil temperature caused significant increases in transpiration rates of *P. tremuloides* ($p<0.001$), *B. papyrifera* ($p=0.029$) and *P. glauca* ($p<0.001$) and weaker (non-significant) increases in *P. balsamifera* ($p=0.084$) (Figure 2-6b). *Betula papyrifera* and *P. balsamifera* had very different responses to the treatments; *P. balsamifera* transpiration was affected by water table but not by soil temperature whereas *B. papyrifera* transpiration responded to soil temperature, but was unresponsive to changes in water table ($p=0.89$). An interaction effect between water table and soil temperature on transpiration rate was observed for *P. glauca* and *P. tremuloides* only ($p< 0.001$and $p=0.009$, respectively). Transpiration for these two species was greatest in the low water table and 22°C soil temperature treatment. Transpiration rate in *P. tremuloides* was approximately twice that of *P. glauca* (2.50 mmol m^{-2} s^{-1} vs. 1.31 mmol m^{-2} s^{-1}) in this treatment combination (Figure 2-7).

Discussion

The results of this study showed that the four boreal tree species varied considerably in seedling response to both water table level and soil temperature. Overall, all four species studied generally grew larger (i.e. performed better) and had higher transpiration rates in the warm soils (12 and 22°C) and the low water table treatments. However, species response to variation in water table level and soil temperature differed, and generally fell into one of three patterns (Figure 2-6); 1) species that were relatively insensitive to water table variation. *Betula papyrifera* fell into this category. 2); species that were sensitive to water table variation, but relatively insensitive to soil temperature. *Picea glauca* followed this pattern. Lastly, 3); both *P. tremuloides* and *P. balsamifera* were sensitive to variation in both water table level and soil temperature. Thus, these results provide insight into suitability of these species for water table level control on wet boreal sites. In terms of general suitability for control of water table on wet sites, I consider the relative ranking of species I studied to be *B. papyrifera* >*P. tremuloides* >*P. balsamifera* >*P. glauca* and discuss them in that order.

Betula papyrifera

High water tables alone did not seriously reduce *B. papyrifera* growth and gas exchange. However, *B. papyrifera* is generally thought to be somewhat flooding intolerant. Indeed, Ranney and Bir (1994) found it the most flooding intolerant species of *Betula* studied including *B. nigra*, *B. platyphylla* var. *japonica* 'Whitspire' and *B. pendula*. Similarly, Tang and Kozlowski (1982) and Tripepi and Mitchell (1984) have also reported flooding intolerance in *B. papyrifera*. However, *B. papyrifera* was clearly the most flooding tolerant of the boreal species I studied. Many studies have used inundation, flooding at or above the soil surface, to test for flooding tolerance, whereas my study dealt with water tables that were below the soil surface so this could be a factor in my contrasting results. Although, Iremonger and Kelly (1988) studied the response of *B. pubescens* to very high water tables (both inundated and 5 cm below the surface) and found reduced growth in both levels when compared to a control, their flooding treatments were more severe than the ones I imposed. Additionally, many researchers have studied the effect of

soil temperature on *Betula spp.* and found it to be generally tolerant of cold soils (Lyr 1984, Tang and Kozlowski 1982), although it often performs best at warmer temperatures (Tsukahara and Kozlowski 1986, Heninger and White 1974). This general observation is consistent with my findings. However, the response of *B. papyrifera* to soil temperature is highly dependant on water table level.

In my study, when soil temperature remained at a constant moderate temperature, water table had little effect on growth and transpiration of *B. papyrifera:* However, reduced growth and transpiration occurred when *B. papyrifera* was grown in both a high water table and a high temperature. But when soil temperatures were low, *B. papyrifera* grew better in the high water table level. Tsukahara and Kozlowski (1986) also studied flooding and temperature and supposed that reduced growth at higher temperatures and flooded conditions could be due to decreased capacity of water to hold oxygen as its temperature increases as well as increased soil oxygen depletion at higher temperatures. However, Tsukahara and Kozlowski (1986) found that the effect of flooding was more important than the effect of soil temperature on birch whereas I found that temperature was the significant factor affecting *B. papyrifera* growth. Tsukahara and Kozlowski (1986) imposed a water table level of 4 cm above the surface and this extreme flooding may have contributed to their result.

My study indicates that if moderate temperatures can be anticipated, such as found in clearcuts in central Alberta, then *B. papyrifera* would be able to withstand variations in water table level up to within 10 cm of soil surface. This would make it suitable for planting in a high water table site condition, but not necessarily an inundated condition. In a boreal mixedwood clearcut, summer soil temperatures were found to be above 10°C, and as high as 14 °C, from June 20 to August 30 (Chapter 3) which appear to be a suitable range for *B. papyrifera* growth at both high and low water table levels.

Populus tremuloides

In contrast to *B. papyrifera*, transpiration in *P. tremuloides* was strongly reduced by the high water level. Similarly, cold soils had a strong negative affect on growth and gas

exchange. The negative effect of cold soil temperatures on *P. tremuloides* gas exchange and growth variables has also been documented by others (Tyron and Chapin 1983, Wan et al. 1999, Landhäusser et al. 2001). For instance, Tyron and Chapin (1983) found that of six taiga species, *P. tremuloides* had the most temperature sensitive roots. Wan et al. (1999) reported very low root water uptake at soil temperatures of 5°C and 10°C, which had a negative impact on shoot and root growth rates. However, in my study *P. tremuloides* seedlings grew best in low water tables, when the soil temperature was above at least 7.5 °C. Additionally, *P. tremuloides* did not respond negatively to the combination of warm soils and high water tables. This is in contrast to the response of *B. papyrifera* to this treatment combination. The positive response of *P. tremuloides* is consistent with the findings of Agafonov (1995) on the floodplain of the Ob' River, where increased growth of *Populus tremula* L. was found under flooded conditions due to the warming effect of the warm river water.

The leaf area development of *P. tremuloides* and *B. papyrifera* in the various treatments were similar. However, the reduced transpiration and growth of *P. tremuloides* in both high water table and cold soils, compared to the ability of *B. papyrifera* to better withstand higher water table levels, suggests *P. tremuloides* is less preferable than *B. papyrifera* for planting in conditions of high water tables, particularly if soil temperatures are cold.

Populus balsamifera

The response of *P. balsamifera* to variation in water table level and soil temperature was generally similar to that observed for *P. tremuloides*. Among the deciduous species, *P. balsamifera* growth was most strongly reduced by high water table levels. This was contrary to my expectations as *P. balsamifera* often occurs in riparian (subject to periodic flooding) (Tyree et al. 1994) and floodplain (Tyron and Chapin 1983) habitats. Though *P. balsamifera* is also considered to have physiological adaptations to wet conditions including rapid physiological recovery after flooding, Amlin and Rood (2001) found reduced growth in inundated *P. balsamifera*. Similarly, Regehr et al. (1975) found reduced photosynthetic rate in another riparian poplar, *P. deltoides*, when flooded.

However, despite the fact that flooded conditions were present, the photosynthetic rate of *P. balsamifera* was as high as in some other species grown under optimal conditions. The observations of Regehr (1975) support my study by showing that absolute rates of both net assimilation and transpiration can be higher than other species, which was what I found: transpiration and net assimilation in my study were qualitatively observed to be somewhat higher in *P. balsamifera* than in *P. tremuloides* in the high water table.

Growth, and to a lesser extent, gas exchange of *P. balsamifera* responded positively to increases in soil temperature. Growth variables of *P. balsamifera* were more strongly reduced in the lower soil temperature than growth variables of both *P. tremuloides* and *B. papyrifera.* In contrast, Tyron and Chapin (1983) found that *P. balsamifera* roots had greater elongation at low soil temperatures (<5, 5 and <10°C) than *P. tremuloides*. Even though the lower soil temperatures (7.5 and 12°C) reduced gas exchange compared to the highest soil temperatures in *P. balsamifera*, transpiration rate of *P. balsamifera* was still greater than transpiration rates of all species in warm (12°C) soil treatments.

Transpiration rates of *P. balsamifera* followed the same pattern as *P. tremuloides*, both species' transpiration rates were generally greater at higher soil temperatures and at the lower water table level. However, in the low water table and 7.5°C soil temperature, *P. balsamifera* had the highest transpiration rate of all species, (1.82 mmol m^{-2} s^{-1}), compared to both *P. tremuloides* (0.38 mmol m^{-2} s^{-1}) and *B. papyrifera* (0.44 mmol m^{-2} s^{-1}). These results, while dramatic, need to be viewed cautiously because the sample size of *P. balsamifera* in the low water table and 7.5°C combination was only 2 seedlings compared with between 4-8 for all other species in all treatments. The low sample size was probably due to the fungus observed on these seedlings. This fungus attacked *P. balsamifera* seedlings in all treatment combinations and it is unclear whether the higher mortality rate of *P. balsamifera* seedlings in this treatment combination was a result solely of the fungus, or if the treatment was responsible, or if the interaction effect between the fungus and treatment affected survival of *P. balsamifera* seedlings. However, presuming that the mortality from fungus was independent of treatment effect, the results from surviving seedlings indicate that *P. balsamifera* could maintain higher

net assimilation rates than *P. tremuloides* and *B. papyrifera* at colder temperatures but only when water table is low. However, compared to the other deciduous species in low water table and 7.5°C treatment, the leaf area of *P. balsamifera* was much less than *P. tremuloides* and *B. papyrifera* (83.5 vs. 342.5 and 254.7 cm^2, respectively) which indicates that its overall performance was indeed reduced. In the other treatment combinations, transpiration rate and leaf area of *P. balsamifera* was similar to both *P. tremuloides* and *B. papyrifera*.

Picea glauca

Consistent with the findings of many others, *P. glauca* responded negatively to high water table level. High water table levels reduced growth of *P. glauca* in my study consistent with findings of Mueller-Dombois (1964) and Kozlowski (1984). Similarly, gas exchange of *P. glauca* was also reduced in the high water table level, consistent with the observations of Grossnickle (1986) and Levan and Riha (1986). Other *Picea* species including *P. abies* (Zaerr 1983) and *P. sitchensis* (Coutts 1981) also exhibit reductions in transpiration and photosynthesis in flooded conditions.

Cold soil temperatures negatively affected *P. glauca* root growth and transpiration rate, but the relative effect of variation in soil temperature was much less than in all other species studied (Figure 5). Other studies conducted on *P. glauca* (Heninger and White 1974, Grossnickle 1986), *Picea abies* (Vapaavuori et. al. 1992) and North-western American conifers in general, (Lopushinsky and Max 1990, Tyron and Chapin 1983, and Nambiar et al. 1979) have also documented reduced root growth of *P. glauca* in cold soils. Interestingly, I did not observe any difference in leaf area or leader growth of *P. glauca* in response to soil temperature. This finding is consistent with that of Landhäusser et al. (2001) who also found that *P. glauca* root growth was reduced in cold soils but leaf area was not.

Picea glauca was also very responsive to the interaction of soil temperature and water table level, showing a greater relative increase in gas exchange and growth at the 22°C temperature and low water table treatment combination than any other species. Since *P.*

glauca generally has a negative response to both high water table and low soil temperature, and has smaller leaf area, I conclude that *P. glauca* would not be able to transpire and use water as much as *P. tremuloides*, *B. papyrifera* and *P. balsamifera* in cold wet soils.

Conclusion

Generally all species had reduced growth and gas exchange at high water tables and low temperatures. However, *B. papyrifera* and *P. glauca* had reduced growth in the high water table and warm soil treatment, but *P. balsamifera* and *P. tremuloides* did not. Interestingly, *B. papyrifera* was the only species insensitive to water table level. In addition, growth of *B. papyrifera* was not affected by cold soil temperatures as strongly as that observed in *P. balsamifera* and *P. glauca*. Therefore, I conclude that *B. papyrifera* would be a suitable species to use as a nurse crop (for *P. glauca*) for water table level control on wet sites. If conditions are suitable, *B. papyrifera* can grow quickly and produce large leaf area in a short time (Tang and Kozlowski 1982).

Since transpiration rates were similar among all deciduous species in the high water table level treatment, the species selected for use as a nurse crop in the field should be the one that could develop the largest leaf area and use the most amount of water and perform well in cold soils. *Betula papyrifera* responds most favourably to the cold and wet soils that may prevail on boreal mixed wood clear cuts because of its ability to maintain a high leaf area in cold-wet soils. It was also able to maintain a higher transpiration and NA rates in cold soils and a high water table than *P. tremuloides* and *P. balsamifera*. *P. tremuloides* would be the next candidate because it can maintain a higher leaf area in cold soils and high water table conditions than *P. balsamifera*, even though the transpiration rates were similar between the two species. *Populus balsamifera* would be next best suited. I observed reduced growth in high water tables, even though it appears very tolerant of cold soils if water tables are low. *Populus balsamifera* would not be suitable for a nurse crop in cold soils with a high water table because even though it could

continue to transpire at a comparable rate, I observed much lower leaf area, which would limit total water use. High water tables would presumably persist on these sites until sufficient water use by the regenerating vegetation is re-established. This would require species that can quickly develop leaf area, but are also tolerant of both flooding and cold soils.

Table 2-1. Number of seedlings per species in treatment combinations

Species	Temperature / Water Level	7.5 °C	12 °C	22 °C
Populus balsamifera	High water table	6	6	4
Populus balsamifera	Low water table	2	4	5
Populus tremuloides	High water table	4	7	5
Populus tremuloides	Low water table	3	6	6
Betula papyrifera	High water table	7	7	6
Betula papyrifera	Low water table	6	8	6
Picea glauca	High water table	7	7	7
Picea glauca	Low water table	7	7	7

Table 2-2. Effects of water table and soil temperature on growth of seedlings

	Water table level			Soil temperature treatment				Water table x soil temperature
Leader growth (mm)	High	Low	p value	7.5°C	12°C	22°C	p-value	p-value
Populus tremuloides	172.3	222.4	0.093	136.2^{a}	193.6^{ab}	262.7^{b}	**0.008**	0.689
Betula papyrifera	170.8	229.9	**0.043**	129.9^{a}	219.8^{b}	251.2^{b}	**0.004**	0.218
Populus balsamifera	128.9	155.5	0.211	86.0^{a}	157.9^{b}	182.8^{b}	**0.005**	0.283
Picea glauca	62.6	78.6	**0.014**	68.2	69.0	74.6	0.620	0.783
Live root dry weight (g)								
Populus tremuloides *	5.12	6.61	0.254	6.44	5.21	5.95	0.805	0.627
Betula papyrifera	4.61	4.97	0.682	4.07	5.20	5.10	0.486	0.213
Populus balsamifera *	2.42	5.21	**0.028**	2.33	3.33	5.80	0.489	**0.020**
Picea glauca	1.24	2.68	**<0.001**	1.36^{a}	1.48^{a}	3.04^{b}	**<0.001**	**<0.001**
Leaf area (cm^2)								
Populus tremuloides *	399.4	551.4	0.085	289.0^{a}	419.1^{ab}	653.6^{b}	**0.025**	0.94
Betula papyrifera	366.8	502.5	0.108	288.2^{a}	424.3^{ab}	606.1^{b}	**<0.001**	0.235
Populus balsamifera	208.1	465.1	**0.024**	129.4^{a}	314.6^{ab}	473.9^{b}	**0.005**	**0.015**
Picea glauca	236.7	267.0	**0.008**	240.7	262.8	252.0	0.64	0.683
Root:shoot ratio								
Populus tremuloides	0.78	0.90	0.263	0.89	0.88	0.74	0.404	0.990
Betula papyrifera	0.52	0.66	0.221	0.58	0.73	0.47	0.182	0.881
Populus balsamifera	0.49	0.70	0.092	0.63	0.44	0.71	0.112	0.128
Picea glauca	0.19	0.32	**<0.001**	0.18^{a}	0.19^{a}	0.38^{b}	**<0.001**	**<0.001**

* indicates that ANOVA was performed on log (base 10) transformed data.

For soil temperature treatments, levels with common letters are not significantly different at $p<0.05$.

Table 2-3. Effects of water table and soil temperature on net assimilation and transpiration of seedlings

	Water table level			Soil temperature treatment				Water table x soil temperature
Net assimilation ($\mu mol\ m^{-2}\ s^{-1}$)	High	Low	p value	7.5°C	12°C	22°C	p value	p value
Populus tremuloides	2.64	7.48	**<0.001**	2.44^{a}	5.57^{ab}	7.17^{b}	**0.011**	0.172
*Betula papyrifera**	3.16	5.89	0.107	2.84^{a}	5.02^{b}	5.66^{b}	**0.016**	**0.002**
*Populus balsamifera**	3.35	6.01	**<0.001**	4.49	6.61	8.33	0.067	0.111
Picea glauca	1.51	4.92	**<0.001**	2.74^{a}	2.96^{ab}	3.96^{b}	**0.039**	**<0.001**
Transpiration ($mmol\ m^{-2}\ s^{-1}$)								
Populus tremuloides	0.62	1.46	**<0.001**	0.50^{a}	0.93^{a}	1.68^{b}	**<0.001**	**0.009**
*Betula papyrifera**	0.86	1.10	0.89	0.44^{a}	0.93^{ab}	1.57^{b}	**0.029**	0.497
*Populus balsamifera**	0.82	1.74	**0.015**	0.67	1.09	2.09	0.084	0.521
Picea glauca	0.32	0.89	**<0.001**	0.48^{a}	0.56^{a}	0.79^{b}	**<0.001**	**<0.001**

Figure 2-1. Box and pot and reservoir construction for growth chamber experiment

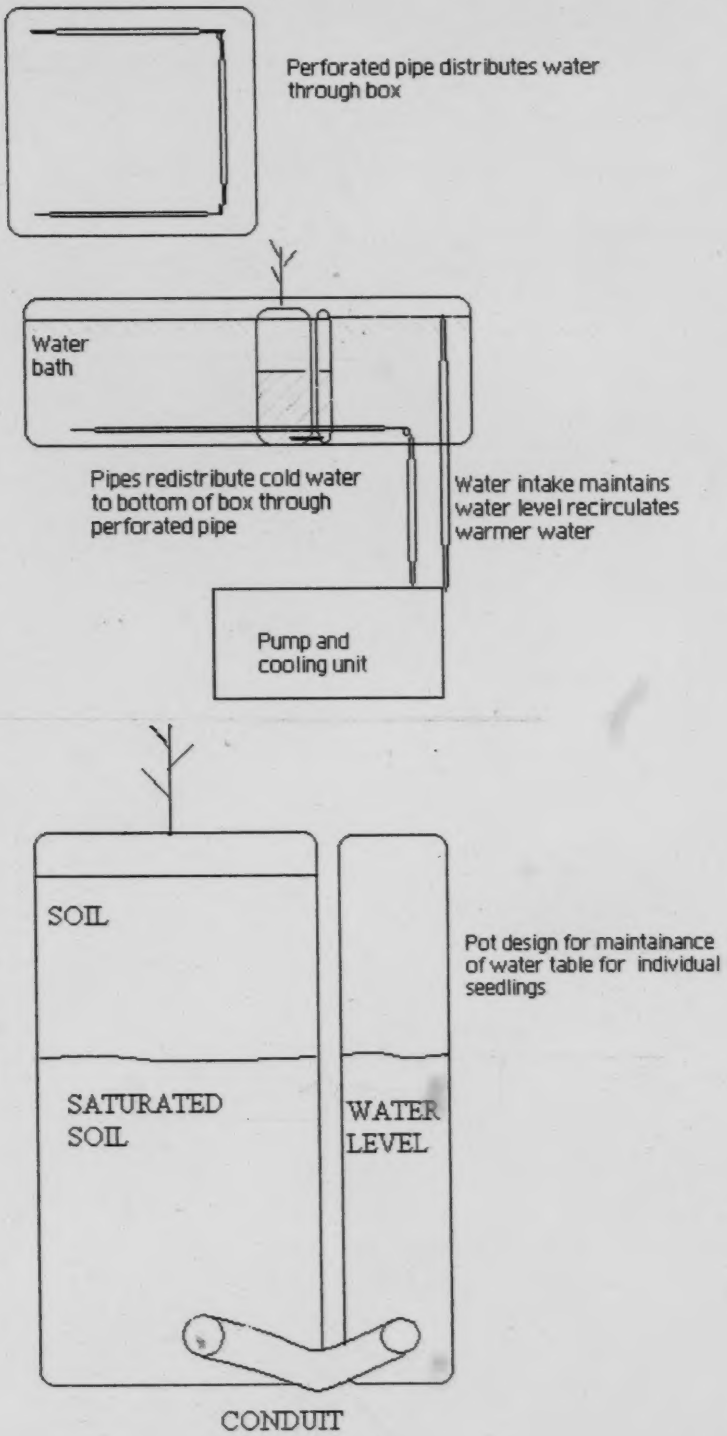
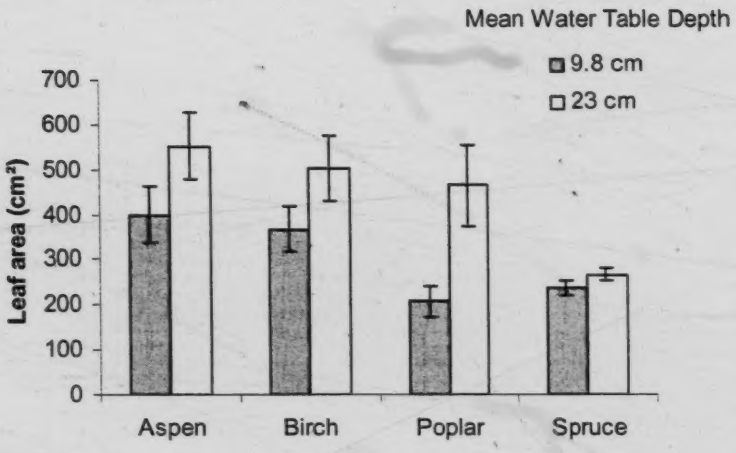

Perforated pipe distributes water through box
Water bath
Pipes redistribute cold water to bottom of box through perforated pipe
Water intake maintains water level recirculates warmer water
Pump and cooling unit
SOIL
SATURATED SOIL
WATER LEVEL
Pot design for maintainance of water table for individual seedlings
CONDUIT

Figure 2-2 2-2a) Mean total new leaf area (cm^2) of seedlings grown at two water table depths from surface). 2-2b) Mean total leaf area (cm^2) of seedlings grown at three soil temperatures (°C). Error bars indicate one standard error of the mean.

a)



b)

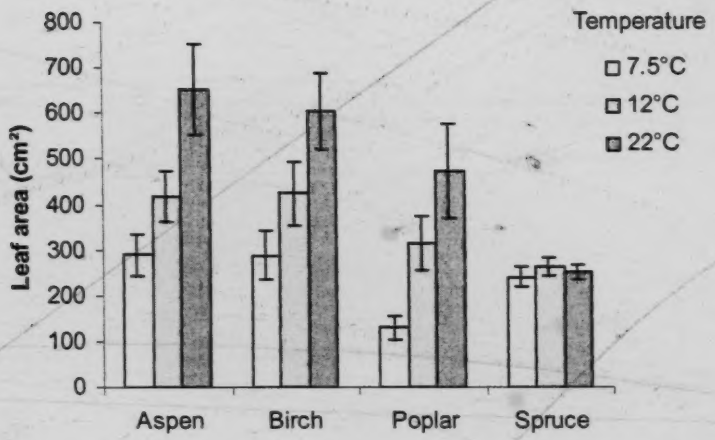


Figure 2-3. Mean live root weight (g) of seedlings grown at two water table levels (cm below surface). Error bars represent one standard error of the mean.

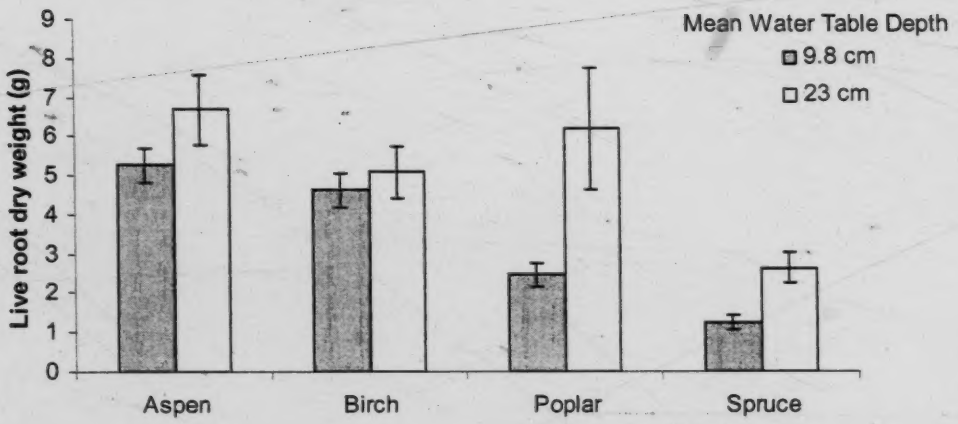


Figure 2-4. *Picea glauca* live root weight (g) in different soil temperatures (°C) in water tables of 9.8 and 23 cm below soil surface. Error bars represent one standard error of the mean.

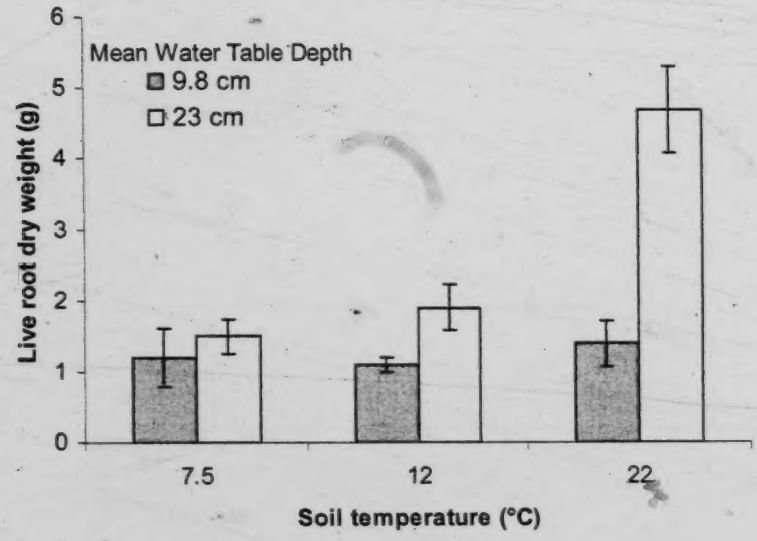
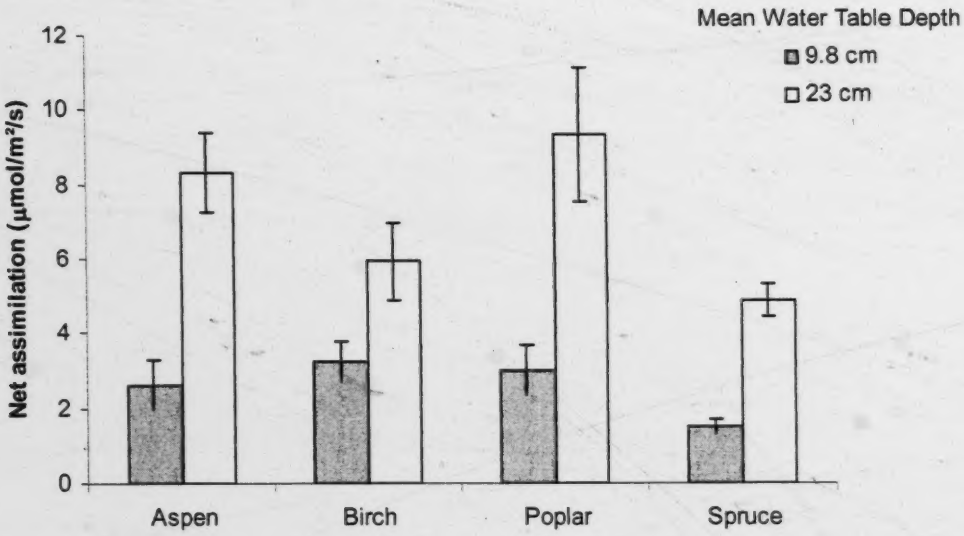


Figure 2-5. 2-5a) Net assimilation (μmol m^{-2} s^{-1}) of seedlings grown at two water table levels (cm below surface). 2-5b) Net assimilation (μmol m^{-2} s^{-1}) of seedlings grown at three soil temperatures (°C). Error bars represent one standard error of the mean.

a)



b)

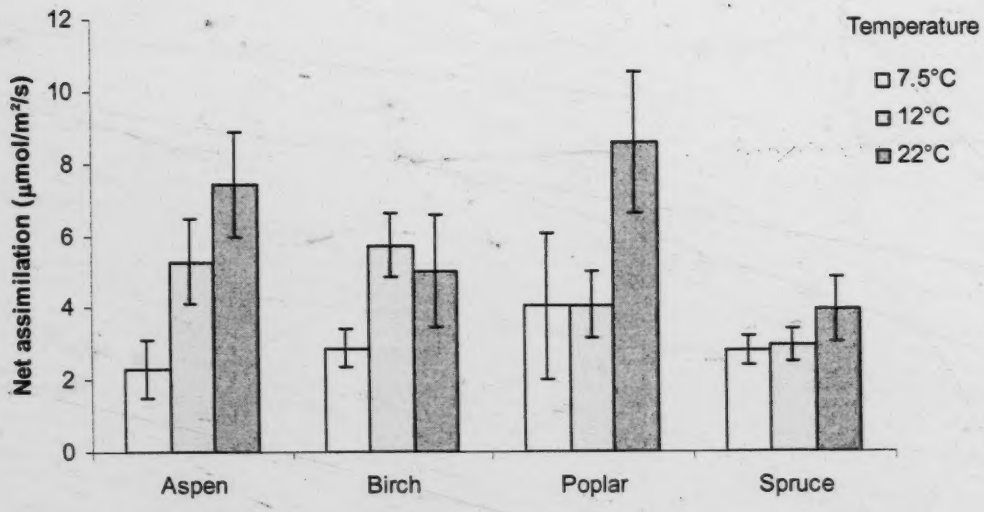
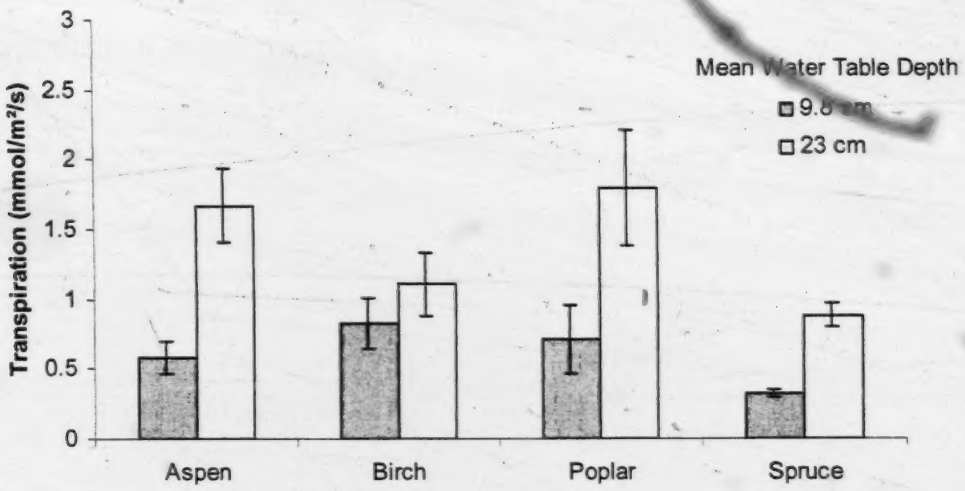


Figure 2-6. 2-6a) Transpiration rates (mmol m^{-2} s^{-1}) of seedlings grown at two water table levels. 2-6b) Transpiration rates (mmol m^{-2} s^{-1}) of seedlings grown at three soil temperatures (°C). Error bars represent one standard error of the mean.

a)



b)

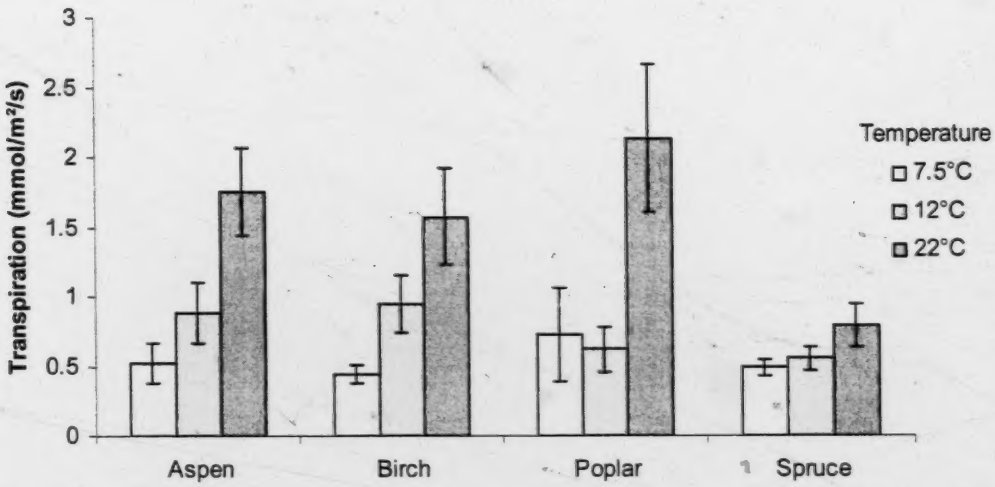
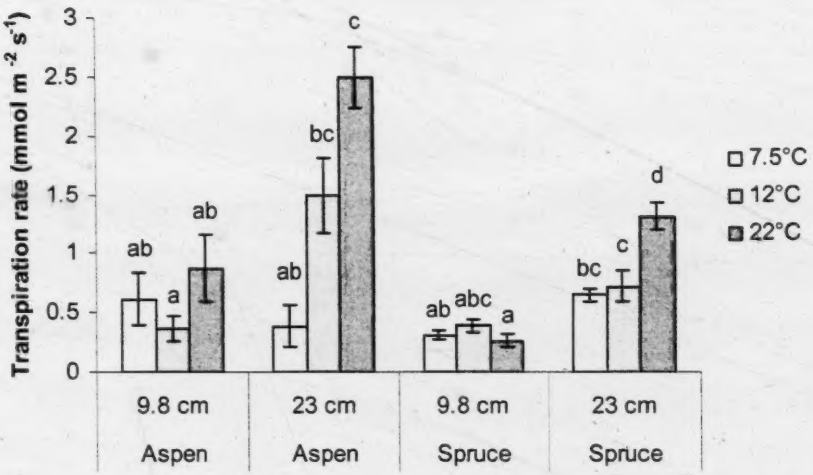


Figure 2-7. Transpiration rate of aspen and spruce at two water table levels at three temperatures. Error bars represent one standard error of the mean. For each species the different letters indicate differences among means ($p \leq 0.05$)



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Chapter 3. Transpiration and growth for four boreal tree species in wet and mesic soil moisture conditions in a mixedwood clearcut

Introduction

On wet mesic to sub-hygric mixedwood sites in the boreal forest of Alberta, *Populus tremuloides* Michx., *Populus balsamifera* L. and *Betula papyrifera* Marsh. Are often found in association with *Picea glauca* (Moench) Voss. These boreal mixed wood stands are generally very productive and are harvested for the large, high quality spruce trees that typically grow best in soils that are not saturated but where available water is rarely limited. After clearcut harvesting, these stands are often affected by high water tables (also referred to as "watering up") (Dubé et al. 1995). The resulting rise in groundwater elevation on these sites can cause delayed conifer regeneration and reduced conifer tree growth (Roy et al. 2001), because *P. glauca* is not well adapted to very wet sites (Eis 1967, Mueller-Dombois, 1964). In addition, the grass *Calamagrostis canadensis* (Michx.) Beauv. often begins to dominate such sites, out-competing both naturally regenerated and planted coniferous tree seedlings (Lieffers et al. 1993). Conventional silvicultural strategies (e.g. herbicide and manual brushing treatments) may provide temporary competition control, but can lead to other silvicultural problems such as persistence of high water tables and the associated problems of poor seedling growth and survival.

In boreal mixedwood forests, the hardwoods *P. tremuloides, P. balsamifera* and *B. papyrifera* dominate early successional stages while *P. glauca* occupy stands in later successional stages (Dix and Swan 1971). One of the ecological functions of pioneer hardwood species in un-managed forests may be to provide relatively rapid water table level control after disturbance. *P. tremuloides, P. balsamifera* and *B. papyrifera* are fast growing trees which could quickly restore water consumption by vegetation on the site thereby aiding in the reduction of water table levels towards pre-disturbance levels or to levels favourable for *P. glauca* regeneration. In addition to water table control, benefits of re-establishing a natural successional pathway would also include increased ground shading. Increased shade reduces the ability of *C. canadensis* to dominate the site

(Lieffers et al. 1993), while *P. glauca* is shade adapted and able to grow under a deciduous canopy (Fries et al. 1997). Thus, planting or allowing for the natural regeneration of a suitably adapted pioneer species may aid in restoring site conditions in which *P. glauca* is able to regenerate successfully.

Previous research has compared the flooding tolerances of boreal trees (both pioneer and later successional species) in growth chamber or greenhouse experiments. Reece and Riha (1991) reported reduced transpiration of eastern larch and white spruce seedlings resulting from flooding. Negative responses to flooding of boreal conifer species were also observed by Levan and Riha (1985) and Zaerr (1983), and Pereira and Kozlowski (1977) report similar findings for several deciduous trees. However, the comparative growth and water use by boreal pioneer species under field conditions is not currently well understood. This understanding would be important for silvicultural strategies using these species as hydrologic nurse crops to control high water table elevations for white spruce re-establishment on wet boreal sites.

The basic question to be addressed by this study is, if deciduous pioneer tree species are planted or allowed to grow, which species has the potential to reduce the water table the fastest to restore a favorable condition for *P. glauca* regeneration. Knowledge of which species is able to take up and transpire the most water largely determines which species is suited for water table control in harvested boreal mixedwood sites. The specific objectives of this study were to examine the effects of variation in water table level on the growth and transpiration of early successional tree seedlings planted in a mixedwood clearcut prepared for *P. glauca* regeneration by mounding. I anticipated that *P. tremuloides*, *P. balsamifera* and *B. papyrifera* would have higher transpiration rates under flooded conditions than *P. glauca*. I anticipated that because the deciduous trees would probably increase their leaf area quickly compared to *P. glauca*. As a consequence, I expected these trees would transpire more water than the slower growing *P. glauca* thus making them more suitable for water table level control than *P. glauca* alone.

Material and Methods

Site Description

The study was conducted approximately 90 km northeast of Lesser Slave Lake (55° 50' N, 114° 20' W) (Figure 3-1a). The study site was a 14 ha cutblock harvested by Zeidler Forest Industries (Alberta Plywood Ltd.) in 1998. *Picea glauca* was the dominant species on the site prior to harvesting with *B. papyrifera*, *P. balsamifera* and *P. tremuloides* present as minor overstory components. The area is quite productive as evidenced by large *P. glauca* in the adjacent un-harvested stands and large (up to 1 m diameter) stumps of *P. glauca* within the study cutblock. The stand was approximately 200 year old judging from growth rings in *P. glauca* stumps remaining after harvesting. Understory shrubs and herbs present, post-harvest, on the site are described in Appendix 1. After harvesting, the site was prepared for planting by mounding as a site preparation technique and the mounds were planted with *P. glauca* (white spruce) seedlings.

Mean annual temperature at Slave Lake is 1.7 °C, and daily mean temperature is 9.7, 13.6, 15.6, and 14.6 °C for May, June, July and August, respectively (Environment Canada, Climate Normals 1971-2000). Average annual precipitation is 497 mm. Mean monthly precipitation is 37.7, 89.8, 96.7, and 69.2 mm for May, June, July and August, respectively (Environment Canada, Climate Normals 1971-2000).

Experimental design

At the time of site selection in mid-May of 1999, the water table was very near the surface. Average water table depth in the mound pits on the sites was 30 cm. I selected twenty microsite plots, each of which was approximately 3 m in diameter, ten of which were in wet microsites with an average water table depth in adjacent mound pits of 17.3 cm. Another ten plots were located in mesic microsites with an average water table depth in mound pits of 42.7 cm. The microsites were located randomly over the cutblock (Figure 3-1b). Each plot was cleared of debris and vegetation to a radius of approximately 1.5 m. Water table monitoring wells (37.5 mm diameter PVC pipes) were

installed to a depth of at least 182 cm. Four additional water table monitoring wells were installed in adjacent un-harvested stands. Two wells were located in the forest on the west side and two on the east side of the clearcut. The two wells were located approximately 50 m and 200 m inside the adjacent unharvested areas.

In each plot (microsite), thermocouples were inserted in the soil at 10 cm and 30 cm depth to measure soil temperature. In order to estimate depth of soil aeration, polished iron rods were inserted 60 cm into the ground. The depth of aeration was determined by the presence of iron oxide along the length of the rod (Silins and Rothwell 1999).

Prior to the 1999 field season, *B. papyrifera* (white birch), *P. tremuloides* (aspen) and *P. balsamifera* (balsam poplar) seedlings were grown from locally (Edmonton area) collected seed in a growth chamber for approximately 5 months. *Picea glauca* (white spruce) (2 yr old stock) were obtained from Weyerhaeuser (Slave Lake). At the end of May, six hardened seedlings of each species were transplanted in each plot after the danger of severe spring frosts had passed (Figure 3-2).

Transpiration measurements

Measurements of transpiration and stem water flow were made using stem sap flow gauges (Dynamax SGA 5 sap flow sensors, from Dynamax Inc. Texas) that employ a heat balance method for determining sap flow. The stem heat balance theory utilized by Dynamax draws on the work of Sakuratani (1981) and Baker and van Bavel (1987) (van Bavel 1994). Utilizing a constant heat input to the stem, and knowing how that incoming heat is partitioned into vertical and radial heat losses, one can determine the portion of the heat that is transported by vertical flow (convection) of the sap. Because the specific heat of water is known (4.186 J g^{-1} $°C^{-1}$), this vertical heat flux can be easily expressed in terms of a mass of water moving up the stem or sapflow (g s^{-1}) as follows:

$$Sapflow = (P_{in} - Q_v - Q_r) / Cp \times dT \qquad [1]$$

Where: P_{in} is the heat input from the stem heater (Watts), and Q_v is the vertical heat convection in two directions, up the stem and down the stem (Watts). Stem cross-sectional area is used in the calculation of this heat loss component (Q_v). Q_r is the heat conducted in the radial direction (Watts) and Cp is the heat capacity of the sap (J g^{-1} $°C^{-1}$). It is assumed that the heat capacity of sap is equivalent to that of water (4.186 J g^{-1} $°C^{-1}$). Finally, dT is the resulting temperature increase of the sap (°C). Because Q_r is not explicitly measured, it must be estimated by solving equation [1] under conditions of zero sapflow. Under these conditions, radial heat loss is governed by radial heat conductance where K_{sh} is the radial sheath heat conductance of the instrument and insulation (W mV^{-1}), and CH is the radial heat thermopile (thermocouples in series) voltage (mV)

$$K_{sh} = (P_{in} - Q_v) / (CH) \qquad [2]$$

Conditions of zero sapflow typically occur during the early morning hours before dawn. Based on my early experience with the technique, I found 3:00 am as the most accurate time during which to estimate K_{sh} based on stability of the readings. Therefore, at least one overnight period was required to get the estimate of K_{sh} to determine sapflow on all seedlings. In the beginning of the first sample period of 1999, I placed the sensors on the seedlings for 24 hours in order to ensure that I observed sap flow in the tree during no-flow conditions. In the second sampling period of the 1999 and thereafter, I felt that a second observation of zero flow conditions was needed because the sensor-stem fit would have more time to adjust after the initial installation. From then onwards I installed the sensors for two complete nights (48 hours) before measurements commenced and used the K_{sh} value from the second night for calculation of sapflow. Once K_{sh} has been empirically determined for a particular sensor/seedling combination, Q_r in equation [1] can be estimated using:

$$Q_r = K_{sh} \times CH \qquad [3]$$

The technique has been favorably calibrated against independent measurements of gas exchange (Zhang et al. 1997) and is becoming a common measurement technique in tree

transpiration studies (Zhang et al. 1999, Allan et al. 1999, Ansley et al. 1994, Hussein and McFarland 1994).

Sapflow data were collected using a CR10 (DNX10) (Campbell Scientific, Logan, Utah) datalogger that was powered by a solar panel and a deep cycle battery. All trees were prepared for gauge installation early in the season by clipping branches and leaves from the main stem to approximately 15 cm from the soil surface. The gauge would be attached approximately 10 cm off the ground. This clipping was done as early in the season as possible to avoid effects of injury during the sampling period (clipping usually resulted in the loss of 1-3 leaves per seedling). Before each gauge was installed, stem caliper at gauge location was measured and used as an input into the datalogger program in the field, along with the individual gauge resistance values (provided by manufacturer). The stems were then lightly smoothed with light sandpaper if necessary to ensure a tight fit. Silicone gel was applied to the interior of the gauges to act as a heat conductor to ensure heat was evenly applied to the stem. Gauges were attached and then insulated with foam insulation and the top of the gauge was capped with putty pressed around the stem of the tree to prevent water from entering the gauge. A sapflow gauge was installed on one seedling of each species (4) ×microsite (2) treatment combination and was used to record 0.5 hr average sapflow (g hr^{-1}) from 7:00-17:00 MDT on one replicate seedling of each treatment combination. Gauges were left on for 48 hours and then moved to another tree (in a different plot), randomly alternating micro-site condition and species to prevent bias due to sensor variability.

During each sampling period, measurements were taken at seven randomly selected plots (each measured for two days) selected from the ten plots prepared for each condition (wet and mesic sites). In this way, 7 replicates (seedlings) of each treatment combination were measured during each sampling period. Each sampling period required approximately two weeks to complete. Three sampling periods were used in 1999; June 20 - July 03, July 20 - August 03, and Aug. 20 - Aug. 30. Two sampling periods were used in 2000 because I observed that by the end of August 1999, the seedling leaves were beginning to

senesce, so sampling at the end of August in 2000 was not necessary. As a result, the two sampling periods in 2000 were during June 20 - July 4, and July 20 -to Aug 4.

Average half hourly transpiration rates per unit leaf area during a four-hour period of peak radiation centered on solar noon (11:00-15:00 MDT) were calculated for each species by expressing the transpiration rate (g hr^{-1}) in units of mmol m^{-2} s^{-1} for ease of comparison with the eco-physiological literature. Diurnal half hourly transpiration rate per unit leaf area was calculated from the half hourly sapflow measurements recorded by the sapflow sensors and the leaf area of the individual seedlings. Total daily water use by seedlings reflects both transpiration rate per unit leaf area and the total leaf area of a seedling. Total daily water use for each seedling was calculated by summing the total water use in each 0.5 hr measurement interval over the period from 7:00-17:00 MDT.

Growth and soil variables

After transpiration measurements were completed on each plot, the trees were harvested and leaf area, average size of leaves, and biomass of stems and leaves were determined. Leaf area measurements were done immediately upon arrival at the laboratory from the field. Leaf areas for deciduous trees were calculated using a leaf area meter (LI-3100, Li-Cor Ltd. Lincoln, NE, USA). Average leaf size for the deciduous species was calculated from leaf area and number of leaves per seedling. Projected spruce leaf area was estimated using a relationship between needle dry mass and projected needle area of sub-samples measured using a computer scanner and imaging software (Sigma Scan 3.0, Jandel Scientific, San Rafael, CA, USA). Leaves and all stems were then dried and weighed after at least 48 hours at 68°C. Soil samples were also taken from each plot at both 10 and 30 cm depths using a bulb planter that sampled a known volume of soil for each collection. Soil samples were placed in plastic bags and sealed. Upon returning to the laboratory, these were weighed wet and then dried at 102°C. for at least 48 hours to determine volumetric soil water content. Water table depth, soil temperature (10 and 30 cm depth), and depth of the aerobic limit were also measured on each plot after transpiration measurements were complete.

Statistical analysis

All data were analyzed using the Analysis of Variance/Multivariate Analysis of Variance (ANOVA/MANOVA) module of the statistical program STATISTICA (StatSoft, Tulsa, OK). Environmental variables, and leaf area, stem dry weight, average size of leaves, transpiration and flow for each species, were analyzed using ANOVA procedures with year and microsite as main effects. Data were also analyzed for each year separately to explore the main effects of sample period and microsites within each year. This was necessary because 1999 had three sample periods and 2000 had two sample periods resulting in an unbalanced experimental design. Analysis for an interaction effect between microsite and sample period was not performed for aspen data in 2000 due to missing data for this treatment combination, which was not discovered until after the 2000 field season. Differences among species were examined qualitatively by comparing relative strength of treatment factors across species. Transpiration and sapflow data were analyzed using multivariate ANOVA with repeated measures (MANOVA) because the same seedling was measured over the course of a day. Time of day (7:00-17:00 MDT) and julian day (in the case of individual seedlings measured for more than one day) were treated as within subject factors in the repeated measures analysis. All other treatment factors were treated as between subject factors. Sapflow data were analyzed using data collected every half hour and totaled for the time period: 700 to 1700 to estimate the total water consumption of each species. Transpiration during the period of peak radiation was analyzed on data collected every half hour between the period 11:00 to 15:00 (inclusive) to highlight differences in treatment responses among species. If significant results were observed, a least significant difference test (LSD) was performed to determine where the differences lay within year, micro-site, and sampling period treatment factors. A result was considered significant if $p \leq 0.05$.

Results

Environmental variables

The growing season of 1999 was dry, receiving 262.3 mm of precipitation during the period from May-Sept. at nearby Marten Creek compared to 405.6 mm during the same period in 2000 (Canadian Daily Climate Data)

This was reflected in much lower mean seasonal water table levels in 1999 than in 2000 ($p<0.001$) (mean water table depth was 70.8 and 22.3 cm below the surface in 1999 and 2000, respectively; (Figure 3-3a). The mean water table depth in wet microsites was 37.2 cm below the surface compared to 55.9 cm below the surface in mesic microsites over both years ($p=0.009$). Despite the large variation among years, a difference in water table depth of approximately 20 cm was observed between microsites in both 1999 and 2000 (no interaction effect was evident, $p=0.970$). The water table declined steadily during the growing season in 1999 (Figure 3-3b) in both microsites ($p<0.001$). In 1999, lower water table depths were consistently observed in mesic compared to wet microsites ($p=0.011$; but no interaction effect was observed $p=0.399$). In contrast, in the year 2000 (though there were only two sample periods) water table levels increased during the growing season ($p<0.001$). Again, water table levels were approximately 20 cm lower in the mesic microsites compared to the wet microsites ($p<0.001$), and no interaction between sampling period and microsite was observed ($p=0.779$). Water tables in the monitoring wells within the residual stands did not rise higher than 150 cm from the soil surface for the duration of the experiment.

Consistent with observations in water table elevation, the aerobic limit in 1999 was 32.2 cm below the surface compared to 16.7 cm below the surface in 2000 ($p<0.001$), but strong differences in aerobic limit depth were not observed between wet and mesic microsites across both years ($p=0.080$), (Figure 3-4a). No interaction effect between year and microsite was observed for aerobic limit ($p=0.874$). Differences in aerobic limit depth between sampling periods generally paralleled those observed for water table

depth. In 1999, aerobic limit deepened as the season progressed ($p<0.001$), and during this relatively dry season, the aerobic limit depth was closer to the surface in wet compared to mesic microsites ($p=0.037$). In 2000, the aerobic limit was deeper in the first sample period, $p=0.013$, but differences between the wet and mesic microsites were not strongly evident ($p=0.078$; Figure 3-4b). Relative differences in aerobic limit depth between microsites did not vary across sample period in either 1999 or 2000 (no interaction effect was observed).

The variation between the two years was also evident in soil moisture measurements. Higher soil moisture content was observed in 2000 than in 1999 ($p<0.001$). As expected, wet microsites had consistently greater soil moisture than mesic microsites (Figure 3-5a) in both 1999 and 2000 ($p=0.009$). No interaction between year and microsite was observed. In 1999, soils in both microsites dried out over the season ($p<0.001$) while soils in wet microsites remained wetter than those in mesic microsites for the duration of the summer ($p<0.001$). In contrast, in 2000 soil moisture increased as the season progressed ($p=0.002$) (Figure3- 5b). As in 1999, soil moisture contents in wet microsites were consistently greater compared to mesic microsites ($p<0.001$). No interactions for soil moisture between sample period and microsite occurred in either 1999 or 2000.

Despite strong differences in precipitation, water table level, and soil moisture between 1999 and 2000, mean soil temperature (10 and 30 cm depth) did not differ between years. Mean soil temperatures in the wet microsites did not differ from that in the mesic microsites in either year (Figure 3-6). Furthermore, no interaction effects for mean soil temperature between year and microsite were observed. Soils in 1999 warmed as the growing season progressed ($p<0.001$). Soil temperature decreased with depth in both years and in both the wet and dry microsites ($p<0.001$). Wet microsites were also consistently warmer at 30 cm depth than mesic microsites in both years ($p=0.010$).

Growth variables

Total leaf area of both *P. tremuloides* and *P. balsamifera* was greater in 2000 when compared to 1999 ($p=0.046$ and $p=0.022$, respectively) (Figure 3-7a and 3-7b). In contrast, leaf area of *B. papyrifera* and *P. glauca* was not different between years ($p=0.31$ and $p=0.204$, respectively). No significant difference in leaf area was observed for any species between microsites in either of the two years. In 1999, leaf area of *P. tremuloides* increased ($p=0.002$) as the season progressed through the three sample periods. In 1999, total leaf area of *B. papyrifera* and *P. balsamifera* decreased from the first two sample periods to the third sample period, ($p=0.012$, $p=0.003$ respectively). Total leaf area of *P. glauca* did not vary across sample periods in 1999. No sample period or microsite effects on leaf area were observed for any species in 2000. Furthermore, no interaction between leaf area and any of the treatment effects was observed over both years or within either year. Qualitatively, no differences in total leaf area among species appeared evident in 1999, but by 2000 the total leaf area of both *P. tremuloides* and *P. balsamifera* had increased by approximately 30 % compared leaf area in 1999.

Leaf size reduction over time can be due to flooding stress conditions in seedlings (Kozlowski 1984). As water table rose from 1999 to 2000 leaf size for *P. tremuloides*, *P. balsamifera* and *B. papyrifera* decreased ($p<0.001$ for all three species; Figure 3-8a and 3-8b). However, there was no effect of microsite on size of leaves for any species over the two year period ($p>0.354$ for all species). In 1999, the average leaf size of *P. tremuloides* increased in the second and third periods ($p<0.001$), but interestingly, leaf size of *P. balsamifera* decreased in sample periods two and three. No effect of sample period or microsite on leaf size was noted for *B. papyrifera* in 1999. No interaction between sample period and microsite were observed for any species in 1999. In 2000, average leaf size of *P. balsamifera* and *B. papyrifera* increased from sample period one to sample period two ($p=0.027$ and $p<0.001$, respectively). The average leaf size of *B. papyrifera* was also affected by the interaction between sample period and microsite. The leaf size of *B. papyrifera* was significantly larger in the mesic microsites in the second period of 2000 than in any other treatment combination in 2000. ($p=0.035$).

Variation in dry weight of all stems can indicate differences in growing conditions among treatments. Increases in total stem dry weight, not including leaves, from 1999 to 2000 were observed for *P. tremuloides* ($p<0.001$) but decreases in stem weight occurred for *B. papyrifera* ($p<0.001$) and *P. glauca* ($p=0.003$) over the same period (Figure 3-9a and 3-9b). No change in stem dry weight between years was observed in *P. balsamifera* however, *P. balsamifera* was also the only species that responded to microsite condition having significantly heavier stem weight in the wet microsites compared to mesic microsites ($p=0.003$) over both years. No interactions between year and microsite were evident for any species. In 1999, the stem dry weight of *P. balsamifera* was greater in wet microsites (4.97 g) compared to the mesic microsites (3.88 g) ($p=0.005$). Following the same trend, but non-significantly, in 2000 the stem dry weight of *P. balsamifera* did not differ between microsites. Overall, stem dry weight generally increased during the growing season in both years for all species and no interactions between year and microsite or sample period and microsite for 1999 and 2000 existed for any species.

Water use variables

The average maximum transpiration rate per unit leaf area of *B. papyrifera*, calculated from 11:00 to 15:00 daily, was lower in 1999 (3.4 mmol m^{-2} s^{-1}) than in 2000 (1.51 mmol m^{-2} s^{-1}, $p<0.001$, Figure 3-10a and 3-10b). Conversely, the average maximum transpiration rate for *P. tremuloides* was higher in 1999, 3.17 mmol m^{-2} s^{-1}, compared with 2.44 mmol m^{-2} s^{-1} in 2000 ($p<0.001$). Similarly, the daily maximum transpiration rate of *P. glauca* also declined from 1999 to 2000 (2.14 mmol m^{-2} s^{-1} in 1999, 1.69 mmol m^{-2} s^{-1} in 2000) ($p=0.015$). No difference ($p=0.914$) in the average maximum daily transpiration rate of *P. balsamifera* was observed between years (2.82 and 2.99 mmol m^{-2} s^{-1} for 1999 and 2000, respectively). No significant effect of microsite on any species transpiration rate was observed over the two years. However, average maximum daily transpiration rate in *P. balsamifera* was higher in the wet compared to the mesic microsites in 1999, resulting in a significant microsite by year interaction ($p=0.015$) (Table 3-1)

Maximum average daily half hourly transpiration rate of *P. tremuloides* increased from first to last sample period in both 1999 ($p=0.006$, data not shown) and in 2000 ($p=0.012$). Similarly, maximum transpiration rates increased during the 1999 growing season in *B. papyrifera* ($p<0.001$) and *P. glauca* ($p=0.004$). During 1999, *B. papyrifera* seedlings had a higher maximum transpiration rates in the wet microsites (2.32 mmol m^{-2} s^{-1}) compared to the mesic microsites (1.32 mmol m^{-2} s^{-1}) ($p<0.001$), while an interaction effect of sampling period and micro-site was observed ($p<0.001$) for *P. glauca* due to very high transpiration rates in the mesic micro-sites during the third sample period (2.49 mmol m^{-2} s^{-1}). In 1999, the average maximum transpiration rate for *P. balsamifera* was highest in the second sampling period ($p=0.021$). In 2000, however, no differences in transpiration rate of *B. papyrifera, P. glauca,* or *P. balsamifera* were observed between the two sample periods.

Total daily sapflow for *P. tremuloides*, *B. papyrifera* and *P. glauca* was not significantly affected by differences in microsites or sampling year. However, total daily sapflow was higher in *P. balsamifera* in 2000 (wet year), at 62.48 g day^{-1} compared with 33.05 g day^{-1} in 1999 ($p=0.005$) (Figure 3-11). Furthermore, no interaction effects on total daily sapflow were observed between year and microsite for any of the species. In 1999, the total daily sapflow of *P. tremuloides* was least in the first sample period, 21.38 g day^{-1} ($p=0.008$) compared with the second and third sample periods (51.68 g day^{-1} and 53.77 g day^{-1}, respectively). Total daily sapflow of *P. tremuloides* in 2000 was not affected by sample period or microsite condition. No effect of microsite or sample period was observed for total daily sapflow for *B. papyrifera* or *P. glauca* in 1999 or 2000. No effect of microsite or sample period on total daily sapflow of *P. balsamifera* was observed in 1999, however in 2000, seedlings in the second sample period had greater total daily sapflow (78.85 g day^{-1}) than during the first sample period (44.36 g day^{-1}, $p=0.046$). No interaction effects on total daily sapflow between sample periods and microsite were observed for any of the species.

Generally speaking, the largest differences in soil moisture, water table levels, and resulting differences in both transpiration rates and sapflow were observed between the drier growing season of 1999 and the wetter season of 2000. Diurnal patterns of transpiration rate and sapflow are presented in Figure 3-12. Qualitative differences in the diurnal pattern of transpiration rate between years were most evident for *B. papyrifera* where the transpiration rate during the wetter year of 2000 was considerably greater than in 1999 from approximately 9:00 onward. In contrast, *P. tremuloides* and *P. glauca* showed slightly lower transpiration rates from 9:00 onward during the wetter year of 2000 compared to 1999. No consistent differences in the diurnal pattern of transpiration were evident for *P. balsamifera.* However, qualitative differences in the diurnal pattern of sapflow (which reflects the combined effect of transpiration rate and leaf area) indicate that by early to mid-morning, both *B. papyrifera* and *P. balsamifera* had higher sapflow during 2000 (wetter year) than during 1999. In contrast (and similar to diurnal patterns of transpiration), sapflow of *P. glauca* was higher during 1999. No consistent difference in the diurnal pattern of sapflow was evident for *P. tremuloides.*

Discussion

The precipitation patterns of 1999 and 2000 provided this study with strongly contrasting water table and soil moisture conditions. The variation in water table and soil moisture was greater between years than between wet and mesic microsite conditions. Additionally, the pattern of water table and soil moisture changes were different within each year. In the dry year of 1999 the water table decreased as the season progressed, while in the wet year of 2000 the water table increased as the season progressed.

These conditions were generally reflected in the response patterns of the four boreal tree species to the different soil moisture conditions. Overall *P. balsamifera* and *B. papyrifera* seemed to be the two species which were able to best cope with the changing soil moisture conditions between these two years, while *P. tremuloides* and *P. glauca* did not respond as favourably to the water table conditions. I conclude that *P. balsamifera* is likely the best species for growth and use as a nurse crop for *P. glauca* in very wet

conditions and potentially waterlogged conditions while *B. papyrifera* was able to cope with moderately wet conditions.

Populus balsamifera appears most suitable to withstand conditions of excess moisture, and seem to have the greatest potential to reduce water table levels in the field due to its relatively high leaf area and greater total sap flow during the wet year (2000). The transpiration rate of *P. balsamifera* was high in the wet microsites in 1999 and the mesic microsites in 2000. During that time the water tables of these two conditions were at about the same depth indicating that planted seedlings of *P. balsamifera* performed best in a range of water table depths between 70 and 30 cm below the surface. For planted seedlings, a water table depth below or above that range negatively influenced *P. balsamifera* transpiration. This is similar to findings presented by Amlin and Rood (2001) who also found reduced transpiration in mature *P. balsamifera* trees grown in inundated conditions for 152 days. However, Harrington (1987) reported no stomatal closure in *P. trichocarpa* Torr. & Gray (another riparian tree species) when seedlings were flooded for twenty days. My study indicates that in the relatively high water table levels that were observed in the field, *P. balsamifera* seedlings were able to maintain transpiration. Liu and Dickmann (1993) report that the flooding of different poplar clones for 18 days did not cause significant short-term changes in photosynthesis and stomatal conductance, although near the end of their experiment, photosynthesis and stomatal conductance were suppressed during midday.

The extremely high water table in 2000 had a negative effect on growth, transpiration, and sapflow on all four species. However, while the overall maximum average transpiration rate in both *P. tremuloides* and *P. glauca* decreased from 1999 to 2000, it remained unchanged for *P. balsamifera* and actually increased in *B. papyrifera.* This likely indicates that *B. papyrifera* prefers the moister soil conditions; however only as long as the soils are not inundated, since during the very wet (second sampling) period in 2000 *B. papyrifera* had reduced transpiration rates. *Betula papyrifera* maintained higher overall transpiration rates during the wet year of 2000 than the other three species, although transpiration declined significantly when water table was higher than 20 cm

below the surface. This finding agrees favorably with other reports that *B. papyrifera* is negatively impacted by waterlogged conditions (Tang and Kozlowski 1982). In addition, Ranney and Bir (1994) found that *B. papyrifera* was the least flood tolerant of four birch species (*Betula pendula*, *B. platyphylla* var. *japonica*, and *B. nigra*) when inundated. The ability of *B. papyrifera* to continue to transpire under wet conditions indicates that it is physiologically well suited for regenerating on wet harvested mixedwood sites. However, leaf area development *B. papyrifera* was slower than in the other two *Populus* species. This indicates that *B. papyrifera* may take a longer time to grow leaf area as great as *P. tremuloides* or *P. balsamifera* and may, at least initially, have less effect on reducing the water table in the first two years than *P. balsamifera*.

The wet year (2000) caused a significant reduction in transpiration rates in *P. tremuloides*. This indicates that of the three deciduous species, *P. tremuloides* is probably the most sensitive to a high water table level and therefore would be least suitable for regenerating in flooded soil conditions. Similarly, *P. glauca* also had reduced transpiration in the very wet year of 2000 and had no increase in leaf area, which renders it least suitable for planting in flooded sites all of four species studied.

Since time is an important factor in the regeneration of forest stands, the hydrological nurse crops should have an ability to quickly establish, survive, and develop large leaf area under these unfavorable conditions for *P. glauca* establishment. Those species that have both high growth and transpiration rates in very wet conditions would likely have the greatest effect on water table elevation in mixedwood sites with high post-harvesting water tables. None of the species studied increased both transpiration and growth during the wet year of 2000 as compared to the previous year. However, *P. balsamifera* showed an increase in leaf area and no decline in transpiration rate, which resulted in *P. balsamifera* being the only species to have increased total daily flow in 2000 compared to 1999. *Betula papyrifera* had an increase in transpiration rate but no increase in leaf area in 2000, but this was a more favourable response to the wet conditions of 2000 than *P. tremuloides*, which actually had a decline in transpiration rate in 2000. Therefore, in

flooded conditions, *P. balsamifera* appears to have the greatest potential for use a hydrological nurse crop for *P. glauca*.

Table 3-1. Table 3-1a) Effect of year and microsite on aspen, birch, poplar and spruce transpiration and sapflow. Table 3-1b) Effect of sample period and microsite on aspen, birch, poplar and spruce transpiration and sapflow for 1999 and 2000

a)

	Year			*Microsite condition*			*Year x Microsite*
	1999	2000	p value	Wet	Mesic	p-value	p-value
Water table level (cm below surface)	70.78	22.30	**<0.001**	37.19	55.89	**<0.009**	0.970
Aerobic limit (cm below surface)	32.2	16.7	**<0.001**	21.70	27.18	0.080	0.874
Soil moisture (% volumetric water)	44.27	66.22	**<0.001**	64.8	45.69	**0.009**	0.427
Soil Temperature (°C)	12.3	12.72	0.411	12.73	12.30	0.406	0.758
Stem dry weight (g)							
Populus tremuloides	2.64	4.56	**<0.001**	3.63	3.57	0.899	0.571
Betula papyrifera	2.80	1.96	**<0.001**	2.38	2.37	0.96	0.206
Populus balsamifera	4.42	5.09	0.096	5.29	4.22	**0.008**	0.987
Picea glauca	6.43	4.56	**0.003**	4.97	6.02	0.089	0.086
Average size of leaves (cm^2)							
Populus tremuloides	10.69	5.92	**<0.001**	8.44	8.17	0.815	0.767
Betula papyrifera	26.46	4.18	**<0.001**	16.48	14.17	0.351	0.16
Populus balsamifera	18.98	5.93	**<0.001**	12.45	12.46	0.994	0.614
Leaf Area (cm^2)							
Populus tremuloides	250.97	355.43	**0.046**	310.97	295.42	0.761	0.292
Betula papyrifera	263.3	212.25	0.31	219.46	256.09	0.465	0.930
Populus balsamifera	286.54	401.66	**0.022**	388.10	305.10	0.116	0.518
Picea glauca	268.85	236.41	0.204	229.86	275.40	0.077	0.179
Sapflow (g/day)							
Populus tremuloides	39.86	45.04	0.610	44.65	40.25	0.664	0.998
Betula papyrifera	23.14	34.32	0.354	19.74	37.71	0.141	0.898
Populus balsamifera	33.05	62.48	**0.005**	55.25	40.28	0.141	0.816
Picea glauca	30.04	19.81	0.086	23.93	25.92	0.734	0.714
Transpiration rate (mmol m^{-2} s^{-1})							
Populus tremuloides	3.17	2.44	**<0.001**	2.83	2.78	0.801	0.155
Betula papyrifera	3.4	1.51	**<0.001**	2.51	2.40	0.681	0.980
Populus balsamifera	2.82	2.99	0.517	3.11	2.70	0.173	**0.015**
Picea glauca	2.14	1.69	**0.015**	1.91	1.92	0.990	0.338

b)

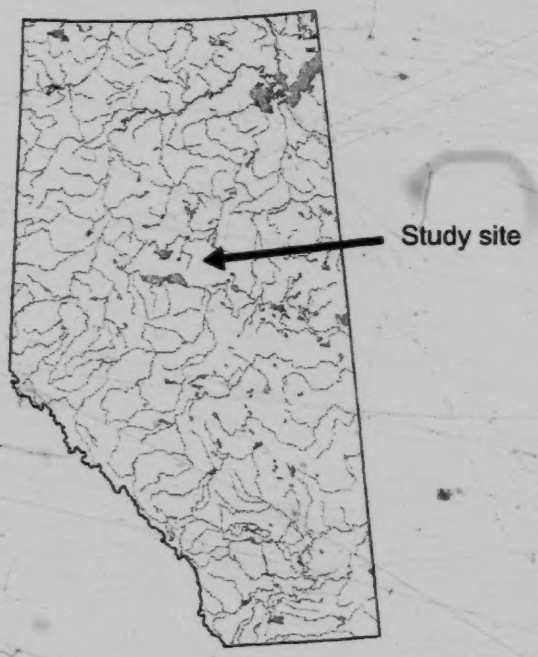
1999	*Microsite*			*Sample Period*				*Microsites x Sample Period*
	Wet	Mesic	p value	1	2	3	p-value	p-value
Water table level (cm below surface)	78.04	57.44	**<0.001**	37.95[a]	79.78[b]	85.49[b]	**0.011**	0.399
Aerobic limit (cm below surface)	29.73	34.71	**0.037**	18.75[a]	30.72[b]	47.2[c]	**<0.001**	0.081
Soil Moisture (% volumetric water)	52.67	35.88	**<0.001**	53.78[a]	42.72[b]	36.33[c]	**<0.001**	0.744
Soil Temperature (°C)	12.44	12.16	0.469	11.39[a]	12.08[a]	13.42[b]	**<0.001**	0.995
Transpiration rate (mmol m^{-2} s^{-1})								
Populus tremuloides	3.45	3.04	0.067	2.79[a]	3.27[ab]	3.69[b]	**0.006**	**0.008**
Betula papyrifera	2.32	1.32	**<0.001**	1.08[a]	1.53[b]	2.84[c]	**<0.001**	**<0.001**
Populus balsamifera	3.13	2.25	0.08	1.85[a]	2.74[ab]	3.47[b]	**0.021**	**<0.001**
Picea glauca	2.09	2.19	0.552	1.79[a]	2.15[ab]	2.49[b]	**0.004**	**<0.001**
Average size of leaves (cm^2)								
Populus tremuloides	11.26	10.64	0.662	5.98[a]	15.04[b]	11.82[b]	**<0.001**	0.998
Betula papyrifera	28.62	22.57	0.347	29.80	23.15	23.84	0.225	0.484
Populus balsamifera	18.43	18.99	0.784	23.89[a]	18.68[b]	13.57[b]	**<0.001**	0.118
Leaf Area (cm^2)								
Populus tremuloides	248.80	274.16	0.568	148.93[a]	331.12[b]	304.38[b]	**0.002**	0.783
Betula papyrifera	208.28	243.38	0.647	373.68[a]	153.18[b]	150.63[b]	**0.012**	0.868
Populus balsamifera	285.40	246.12	0.382	367.55[a]	275.47[a]	154.25[b]	**0.003**	0.796
Picea glauca	265.92	273.43	0.753	274.75	295.8	238.29	0.196	0.151
Sapflow (g/day)								
Populus tremuloides	45.88	38.68	0.442	21.38[a]	51.68[b]	53.77[b]	**0.008**	0.279
Betula papyrifera	17.35	25.04	0.766	31.86	13.88	17.84	0.712	0.604
Populus balsamifera	39.30	23.24	0.183	30.15	44.84	18.83	0.245	0.246
Picea glauca	29.36	33.04	0.648	24.80	35.14	33.67	0.467	0.945
Stem dry weight (g)								
Populus tremuloides	2.60	2.82	0.338	1.27[a]	2.95[b]	3.92[c]	**<0.001**	0.718
Betula papyrifera	2.57	2.97	0.207	2.86	2.73	2.72	0.834	0.488
Populus balsamifera	4.97	3.88	**0.005**	4.32	4.35	4.60	0.788	0.543
Picea glauca	6.62	6.56	0.868	4.61[a]	7.51[b]	7.65[b]	**<0.001**	0.295

b) continued

2000	*Microsite*			*Sample Period*			*Microsites x Sample Period*
	Wet	Mesic	p value	1	2	p-value	p-value
Water table level (cm below surface)	12.82	31.78	**<0.001**	34.07	10.54	**<0.001**	0.779
Aerobic limit (cm below surface)	19.64	33.68	0.078	21.0	12.32	**0.013**	0.428
Soil Moisture (% volumetric water)	79.93	55.50	**<0.001**	56.8	75.63	**0.002**	0.681
Soil Temperature (°C)	13.16	12.42	0.575	12.59	13.0	0.753	0.727
Transpiration rate (mmol m^{-2} s^{-1})							
Populus tremuloides	2.33	2.55	0.426		**Not available, only one sample period**		
Betula papyrifera	3.46	2.76	0.079	3.32	2.90	0.297	**<0.001**
Populus balsamifera	2.85	3.15	0.228	2.87	3.12	0.318	0.565
Picea glauca	1.65	1.69	0.897	1.88	1.46	0.227	**<0.001**
Average size of leaves (cm^2)							
Populus tremuloides	5.88	5.96	0.946	5.91	5.93	0.985	0.412
Betula papyrifera	3.59	4.6	0.178	2.71	5.48	**<0.001**	**0.035**
Populus balsamifera	6.30	5.56	0.364	5.0	6.86	**0.029**	0.412
Sapflow (g/day)							
Populus tremuloides	47.25	42.83	0.822		**Not available, only one sample period**		
Betula papyrifera	26.40	32.73	0.611	18.70	40.43	0.099	0.175
Populus balsamifera	70.2	53.0	0.300	44.35	78.85	**0.046**	0.836
Picea glauca	18.85	17.96	0.924	19.38	17.44	0.836	0.196
Stem dry weight (g)							
Populus tremuloides	4.72	4.40	0.706	3.49	5.62	**0.019**	0.583
Betula papyrifera	2.10	1.82	0.402	1.56	2.36	**0.023**	0.851
Populus balsamifera	5.63	4.63	0.185	4.16	6.10	**0.013**	0.589
Picea glauca	3.50	5.61	0.060	5.56	**3.55**	0.072	0.440
Leaf Area (cm^2)							
Populus tremuloides	390.30	320.56	0.504		**Not available, only one sample period**		
Betula papyrifera	204.68	198.12	0.910	141.25	261.55	0.058	0.991
Populus balsamifera	462.37	329.65	0.143	312.57	479.45	0.070	0.661
Picea glauca	194.15	269.63	0.196	229.86	233.92	0.943	0.522

Figure 3-1. 3-1a) Map of study location. 3-1b) Plot locations within the cutblock study area (W indicates wet micro-sites, D indicates mesic micro-sites).

a)



b)

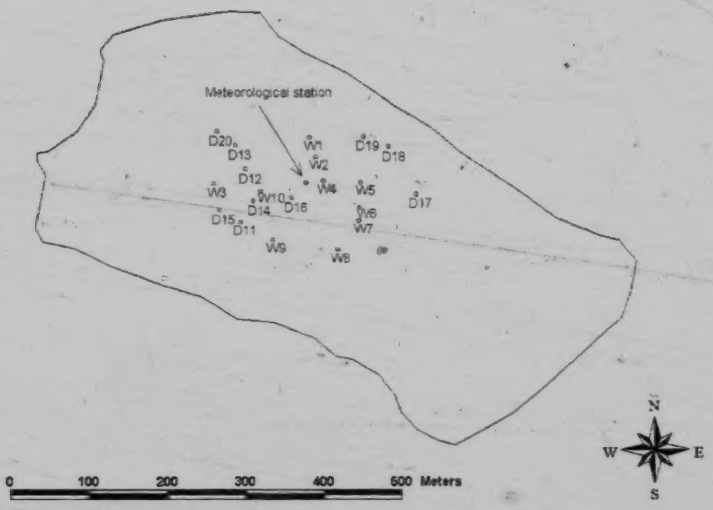


Figure 3-2. Example of plot layout in the field.

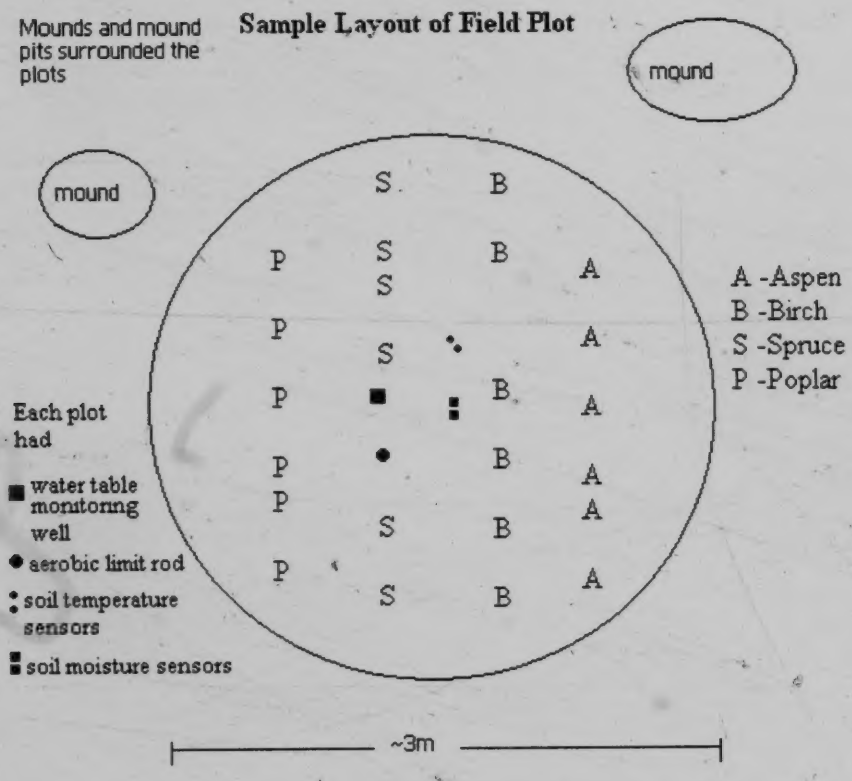
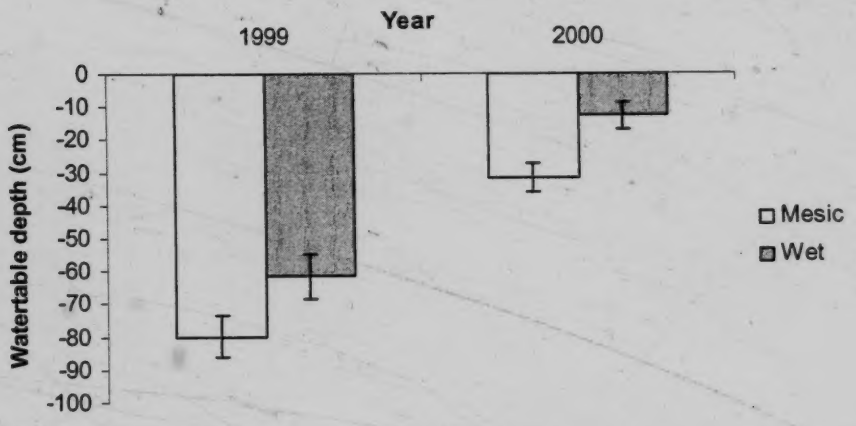


Figure 3-3. 3-3a) Water table level at wet and mesic microsites in 1999 and 2000. 3-3b) Water table depth for wet and mesic microsites, sample periods within 1999 and 2000. Error bars represent standard error of the mean.

a)



b)

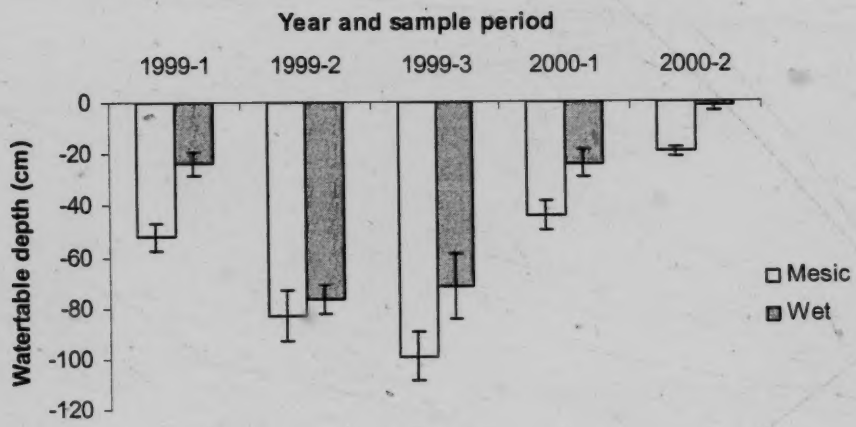
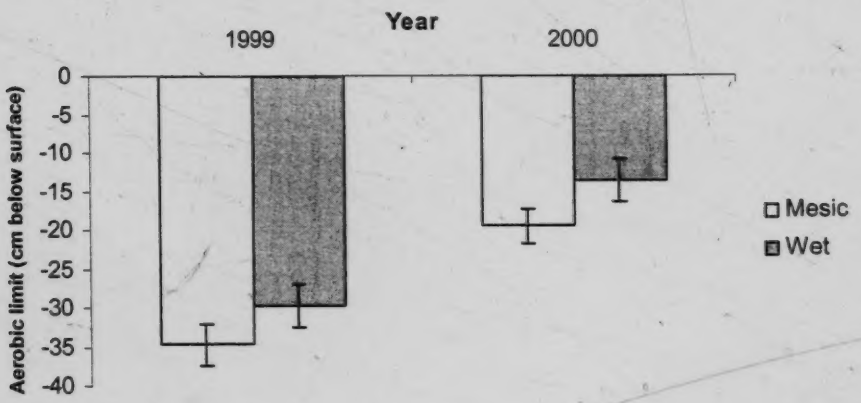


Figure 3-4. 3-4a) Aerobic limit in soil at wet and mesic microsites for 1999 and 2000. 3-4b) Aerobic limit at wet and mesic microsites in sample periods within 1999 and 2000. Error bars represent standard error of the mean.

a)



b)

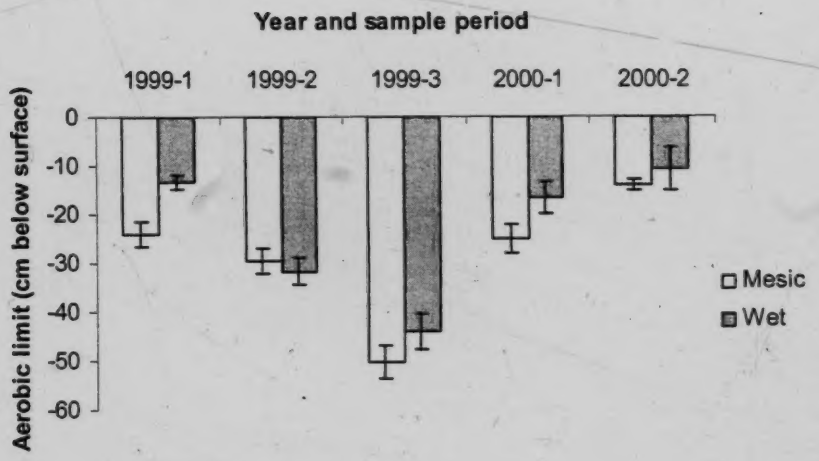
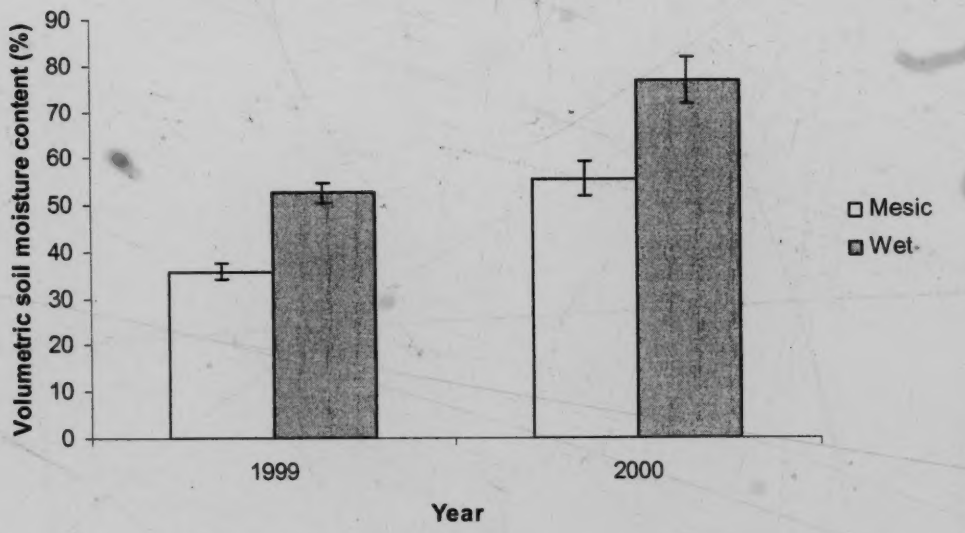


Figure 3-5. 3-5a) Soil moisture in wet and mesic microsites in 1999 and 2000. 3-5b) Soil moisture in wet and mesic microsites for sample periods within 1999 and 2000. Error bars represent standard error of the mean

a)



b)

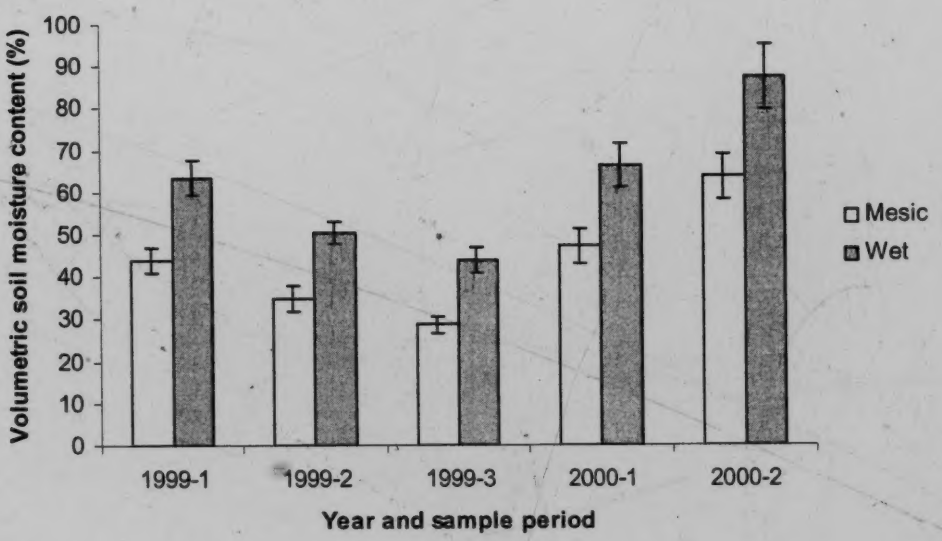


Figure 3-6. Soil temperature in wet and mesic microsites in 1999 and 2000. Error bars represent standard error of the mean.

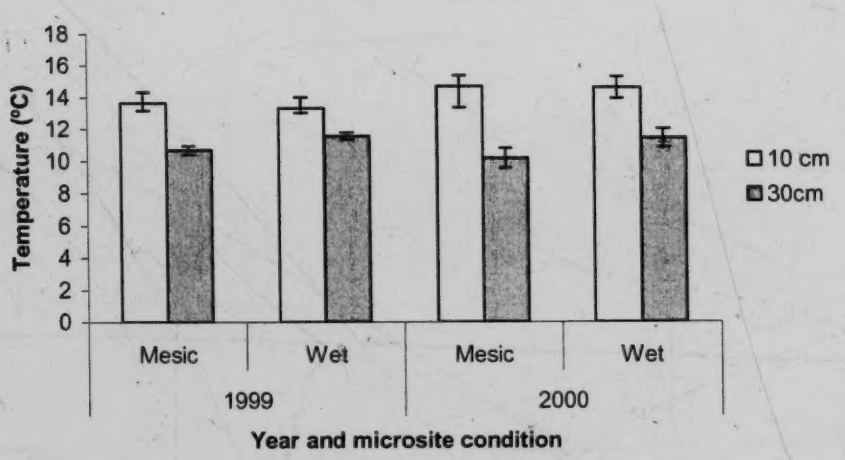
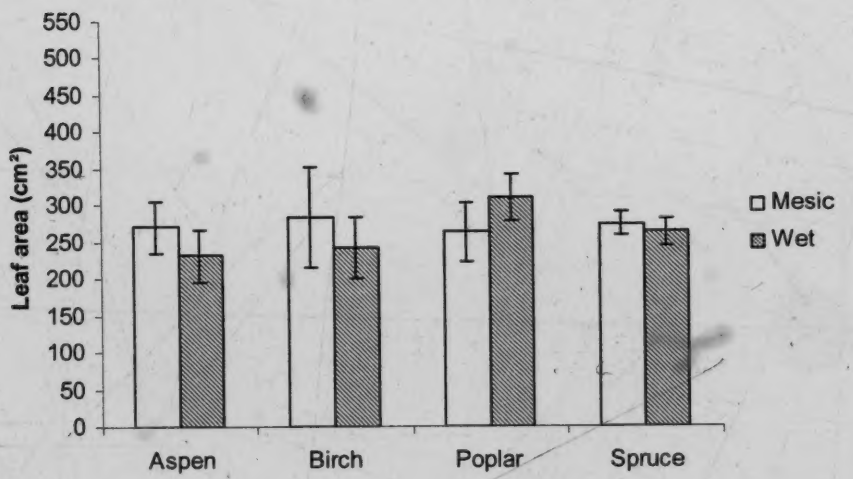


Figure 3-7. 3-7a) Leaf area for aspen, poplar, birch and spruce in 1999 on wet and mesic microsites. 3-7b) Leaf area for aspen, poplar, birch and spruce in 2000 on wet and mesic micorosites. Error bars represent standard error of the mean.

a) 1999



b) 2000

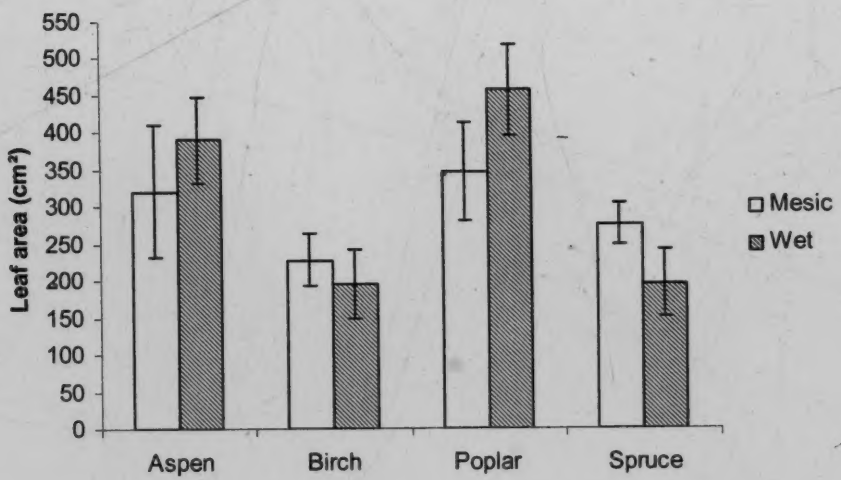
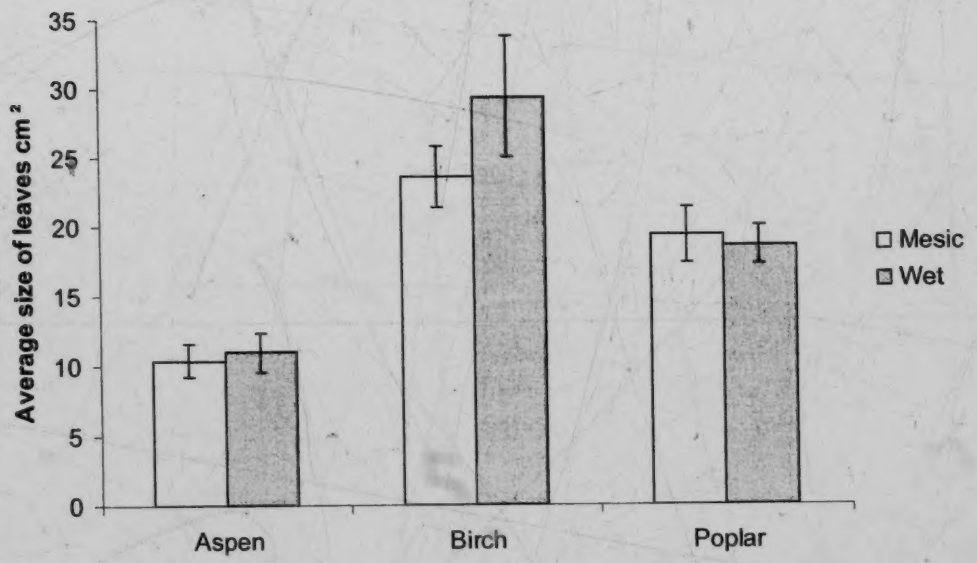


Figure 3-8. 3-8a) Average leaf size for aspen, poplar, birch and spruce in 1999 on wet and mesic microsites. 3-8b) Average leaf size for aspen, poplar, and birch in 2000 on wet and mesic microsites. Error bars represent standard error of the mean.

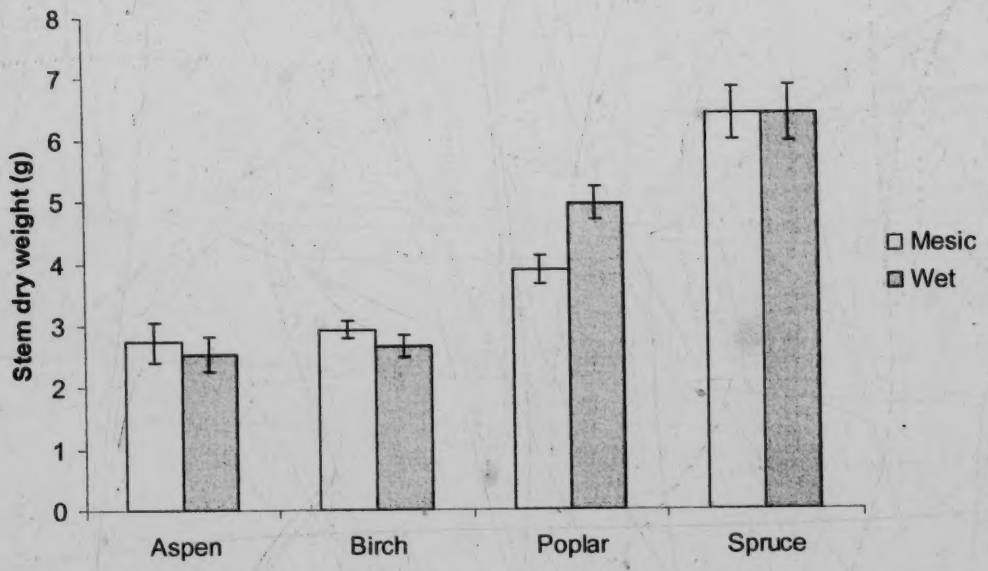
a) 1999



b) 2000

Figure 3-9. 3-9a) Stem dry weight of seedlings in 1999 in wet and mesic microsites.
3-9b) Stem dry weight of seedlings in 2000 in wet and mesic microsites.
Error bars represent standard error of the mean

a) 1999



b) 2000

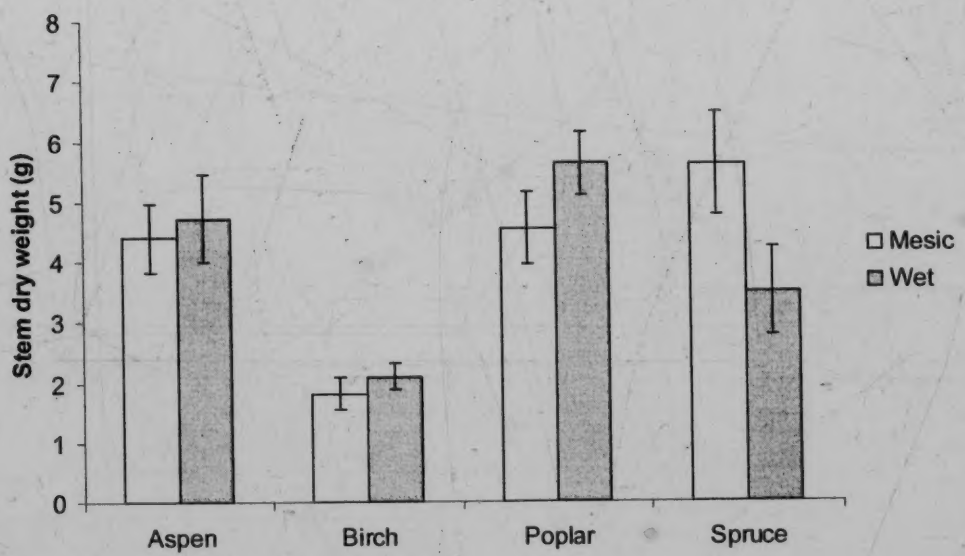
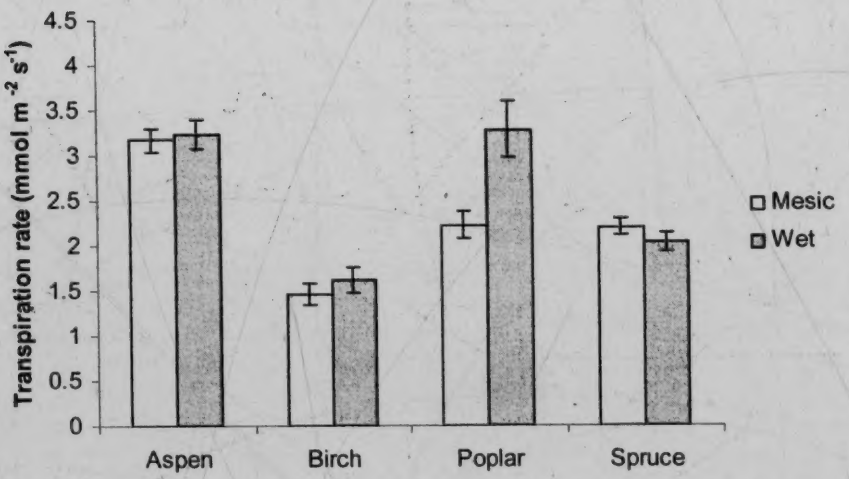


Figure 3-10. 3-10a) Average half hourly transpiration rates of aspen, poplar, birch and spruce in 1999 on wet and mesic microsites (11:00 to 15:00). 3-10b) Average half hourly transpiration rates of aspen, poplar, birch and spruce in 2000 on wet and mesic microsites (11:00 to 15:00). Error bars represent standard error of the mean.

a) 1999



b) 2000

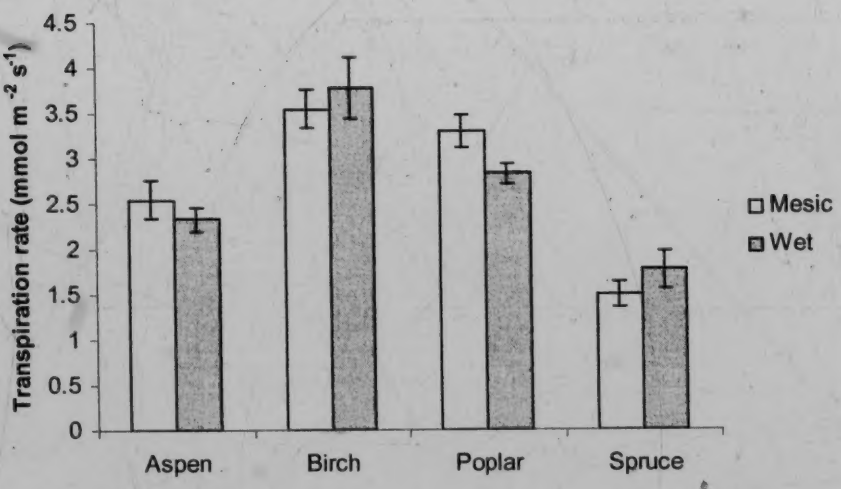
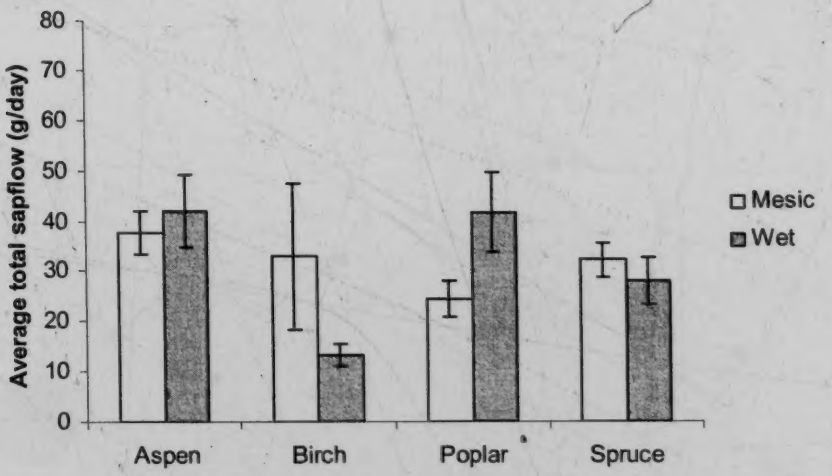


Figure 3-11. Daily (7:00 to 17:00) total water use averages for *Populus tremuloides* (aspen), *Betula papyrifera* (birch), *Populus balsamifera* (poplar) and *Picea glauca* (spruce) in 1999 (3-10a) and 2000 (3-10b).

a) 1999



b) 2000

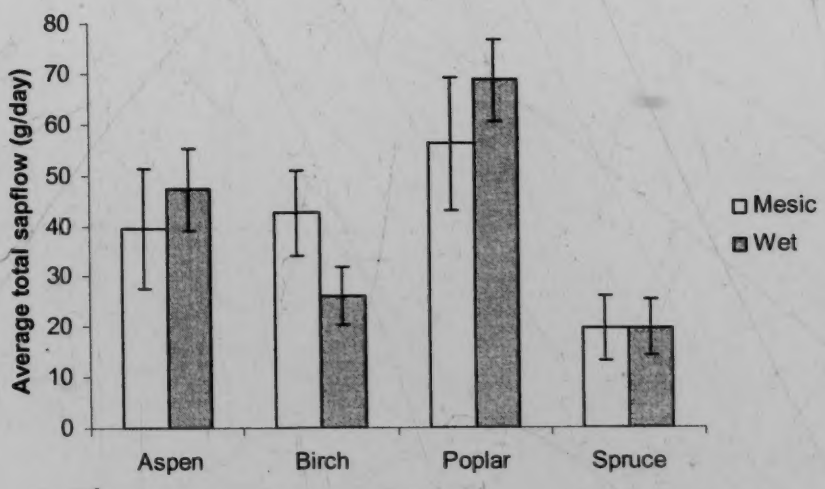
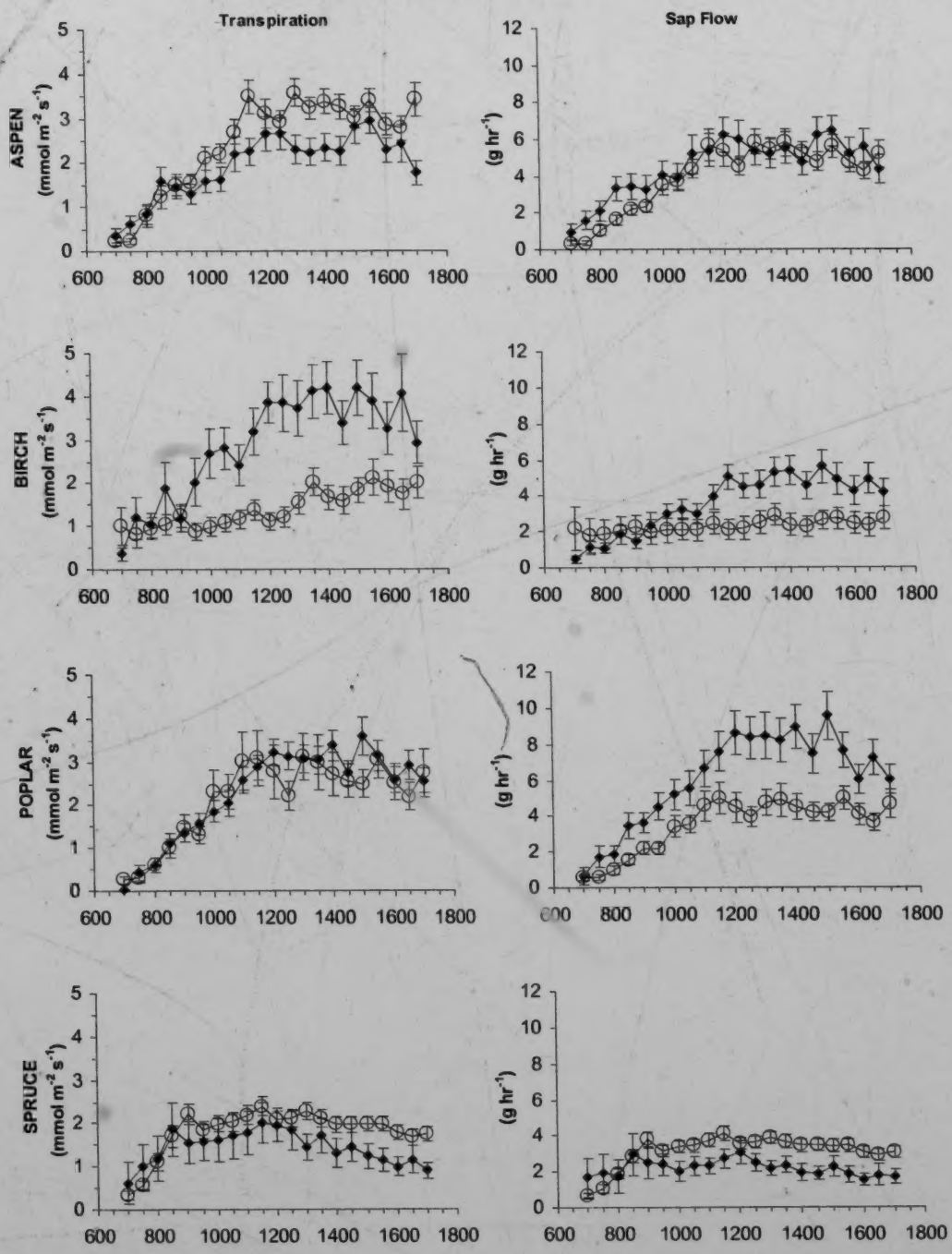


Figure 3-12. Daily transpiration and sap flow for aspen, birch, poplar and spruce for 1999 and 2000 for all sampling periods time period 7:00 to 17:00. One seedling of each species in each microsite measured each day. Circles represent data for 1999 (O) and diamonds (♦) represent 2000. Error bars represent standard error of the mean.



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Chapter 4 Synthesis

This research has provided insight into the unique responses of four boreal tree species to variation in water table levels in the field as well as their responses to the combination of effects from various soil temperatures in high water table levels in a controlled environment. Growth variables and transpiration of three deciduous species (*P. tremuloides*, *P. balsamifera*, and *B. papyrifera*) and one conifer species (*P. glauca*) were studied. The results of this research indicate considerable variation in how various water tables and soil temperatures affect each species. Overall, results from both experiments were consistent with the general autecology and successional strategies that are understood for these species. This information, in turn, provides insight into the relative suitability of each of these species for post-harvest water table level control to aid spruce regeneration on wet-mesic mixedwood boreal sites.

My results from the growth chamber experiment (Chapter 2) indicate that all four species prefer either higher (12 and 22°C) soil temperatures or a lower water table depth (23 cm) in order to achieve maximum rates of growth and transpiration. Consistent with that finding, *P. tremuloides* and *P. glauca* did better on drier soils in the field experiment, whereas growth of *P. balsamifera* and *B. papyrifera* was less hindered by higher water tables than the previous two species. However, some differences in the relative sensitivity to flooding and soil temperature of sensitivity of *P. balsamifera* and *B. papyrifera* were observed between the two experiments. For instance, *B. papyrifera* stood out as the most tolerant to high water table levels and cold soils in the growth chamber experiment, but when seedlings were planted in the field, *P. balsamifera* performed the best in the very high water table conditions (approximately 10 cm below soil surface). The contrasting results from the growth chamber environment could be due to the high mortality of *P. balsamifera* that resulted from a disease that reduced the number of seedlings in the growth chamber (low sample size), which probably limits the inferences possible for that portion of the study. The experimental cold soil temperature treatment in the growth chamber was colder than the field soil temperature conditions observed over the two growing seasons. The differences in soil temperature between the two

experiments were probably a major factor in the greater positive response to high water table levels observed in *P. balsamifera* in the field. In the growth chamber, 7.5°C was too cold for *P. balsamifera*.

Greater leaf area of seedlings growing in soils with high water tables would result in greater total water use per seedling if the transpiration rates per unit leaf area were comparable. In the growth chamber, though the transpiration rates were relatively similar among all of the deciduous species at the high water table levels, *B. papyrifera* developed the greatest leaf area and thus would be able to maintain greater total water use. In the field however, *P. balsamifera* developed the greatest leaf area at the high water table condition and I observed the greatest daily total sapflow in this species in wet year. Furthermore (and contrary to my growth chamber results), the leaf area of *B. papyrifera* did not increase as much as the other species in the high water table of 2000 compared to the drier year of 1999. Overall, in both the field experiment and the growth chamber experiment, *P. balsamifera* and *B. papyrifera* performed better at high water tables than either *P. tremuloides* and *P. glauca*. However, *P. glauca* is a species in which environmental impacts have a delayed response and thus the results from these short term studies may not accurately reflect the true effect of treatment conditions on *P. glauca* as well as they do for the deciduous species.

This research contributes to the body of knowledge regarding both individual species responses to the combined effects of soil temperature and water table and also to the comparative sensitivities of four boreal species to water table and soil temperature in controlled conditions and field conditions. While many studies have evaluated the effect of soil temperature on boreal species (Landhäusser et al. 2001, Heninger and White 1974, Lyr 1996, Tyron and Chapin 1983, Tripepi and Mitchell 1984) and the effect of flooding (Regehr et al. 1975, Tang and Kozlowski 1982, Iremonger and Kelly 1988), fewer studies have focused on the interaction between high water tables and soil temperatures (Tsukahara and Kozlowski 1986, Lieffers and Rothwell 1986), yet soil temperature and water table levels have significant interaction effects that cannot be observed by looking at either element alone. Furthermore, few studies have explored these effects from a

comparative view across species. My research has shown that *B. papyrifera* is very sensitive to high water tables, but only when soil temperatures are high, and that *P. tremuloides* and *P. balsamifera* can continue to increase transpiration at high water tables as temperature rises. However, when moderate soil temperatures are present, as in the field experiment, *P. balsamifera* outperforms both species in high water tables.

The objective of this research was to determine which of the four species I studied was able to maintain high water use. The results of this study will be useful in planning silvicultural prescriptions for boreal mixedwood forests. Currently forest management on clearcut mixedwood sites involves herbicide application and manual brushing where necessary to remove deciduous competition in order to regenerate pure stands of *P. glauca.* The current trend in forest management is moving toward attempts to emulate a natural disturbance patterns in both harvesting and regeneration. Understanding the comparative ability of pioneer species to survive and potentially act as hydrologic nurse crops by reducing water table elevations will be very useful. Though these species have traditionally been viewed in the context of competitors with *P. glauca*, this view may change as the potential role of these species to aid in *P. glauca* regeneration is better understood.

The pioneering status of these deciduous species is known (Roy et al 2001) but the additional knowledge that *P. balsamifera* uses more water compared to *P. tremuloides, B. papyrifera* and *P. glauca* will aid in prescribing silvicultural treatments that both emulate natural establishment patterns and perform an important hydrologic role. This knowledge will provide the ability to influence natural regeneration patterns for commercial benefit. As forest management progresses towards emulation of the natural disturbance and regeneration patterns, commercial management will integrate both hardwoods and softwoods on the same site (Yang 1991). This ecosystem management approach to regeneration would enable a crop of *P. balsamifera* trees to grow and then be under-planted, if necessary, with white spruce. The deciduous crop could be harvested and the spruce left to grow. In this way a two crop rotation could be established. This would potentially alleviate the need for herbicides and manual vegetation competition controls

in addition to providing a suitable habitat for *P. glauca* regeneration. Deciduous vegetation is effective at lowering water table levels in boreal zones (Holstener-Jorgensen 1967) and my research provides insight into which species could have the greatest potential benefit in this regard.

Future research

My study just begins to address the topic of water table level control in the boreal forest from a species specific standpoint by studying the responses of species to water table level and soil temperature. Future investigations can build on my research by explicitly exploring the effect of differing species composition on the actual water table variation in the field. Additionally, the responses of species to the high water table levels in the field should be studied for a longer period of time in order to determine if the same comparative trends I observed continue in the future, or if the species responses change with time (e.g. a species is stunted for the first couple years but then begins to accelerate growth beyond that of the other species). The effect of species on water table dynamics should be studied during the early stand growth phase between the first two years (my study) and the period where maximum water use of mature stands is reached. Another area of useful research would be to determine the combined effect of all herbaceous and shrubby vegetation on post-harvest water table levels. The effect of annual climate changes can have a great impact on vegetation growth and survival as well. Climate prediction is becoming more effective as time passes and may one day prove to be a useful part of silviculture planning. If future climatic patterns can be predicted (e.g. 1-2 years into the future) then management strategies can be applied to ensure the best species is planted on the site for the climatic conditions. For example, if the next year is predicted to be wet, silviculture planning can prescribe *P. balsamifera* but if the year is to be unusually cold, then perhaps, *B. papyrifera* is a better choice, and if the next year or two is to be hotter and drier than usual (e.g. an El Niño year) then *P. tremuloides* may be a suitable choice.

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Appendix 1. Species found in study site, in the clearcut area, summer 1999.

Scientific name	Common name	Percent cover
Achillea millefolium	Common yarrow	<15%
Actaea rubra	Red and white baneberry	*
Alnus crispa	Green alder	*
Aralia nudicaulis	Wild sarsparilla	<15%
Aster puniceus	Purple-stemmed aster	<8%
Castilleja miniata	Indian paintbrush	*
Calamogrostis canadensis	Marsh reed grass	40%
Chenopodium capitatum	Strawberry blight	<5%
Cornus canadensis	Bunchberry	<10%
Cornus stolonifera	Red-osier dogwood	10%
Corydalis aurea	Golden corydalis	*
Epilobium angustifolium	Fireweed	<5%
Equisetum arvense	Horsetail	<10%
Erigeron philadephicus	Philadelpia fleabane	<5%
Fragaria virginiana	Wild strawberry	20%
Galium boreale	Northern bedstraw	10%
Galium triflorum	Sweet-scented bedstraw	<5%
Geum rivale	Purple avens	*
Geranium bicknellii	Bicknell's geranium	*
Gymnocarpium dryopteris	Oak fern	*
Ledum decumbens	Northern Labrador tea	* (transition area to forest)
Lonicera involucrata	Bracted honeysuckle	<25%
Mertensia paniculata	Tall bluebells	30%
Plantago major	Common plantain	<10%

Populus balsamifera	Balsam poplar	25%
Populus tremuloides	Aspen	20%
Potentilla norvegica	Rough cinquefoil	*
Ribus lacustre	Black gooseberry	<15%
Ribus oxyacanthoides	Northern gooseberry	<10%
Rosa acicularis	Prickly rose	25%
Rubus chamaemorus	Cloudberry	<10%
Rubus pubescens	Dewberry	<10%
Salix lutea	Yellow willow	*
Typha latifolia	Cattail	*
Urtica dioica	Stinging nettle	30%
Viola renifolia	Kidney-leaved violet	*

* *species is present, although not in high numbers, < 1% cover*